













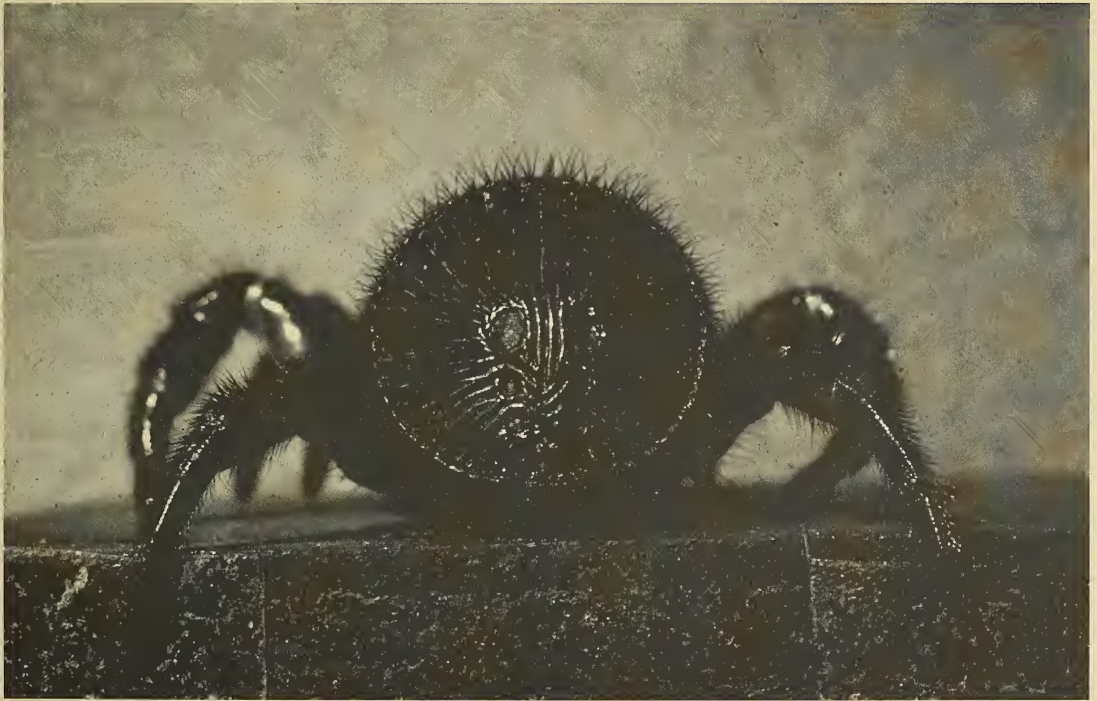
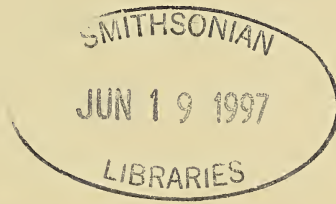




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# The Journal of ARACHNOLOGY

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# THE JOURNAL OF ARACHNOLOGY

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*Cover illustration:* Posterior view of a female trapdoor spider, *Cyclocosmia torreyi*. This spider has been found in Torreya State Park in the panhandle region of Florida, USA. Photo taken about 1950 by a well-known arachnologist, the late H. K. Wallace.

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## DISTRIBUTION, MOVEMENT, AND ACTIVITY PATTERNS OF AN INTERTIDAL WOLF SPIDER *PARDOSA LAPIDICINA* POPULATION (ARANEAE, LYCOSIDAE)

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**ABSTRACT.** The wolf spider *Pardosa lapidicina* Emerton 1885 occupies cobble beaches above the tide line about Narragansett Bay, Rhode Island, USA, and migrates back and forth with the tides. To my knowledge this is the first explicit report of such behavior in a spider. The species is common, attaining densities of over 30 individuals/0.5 m of shoreline. The spiders are confined to the beach from April until November, and 33% or more of the population moves back and forth with diurnal tides during clear or warm weather. Individuals may migrate on one day but remain above the tide line on the next. Small numbers remain on the highest part of the beach through most or all of the winter; others retire into the adjacent coastal scrub. Spiders occupy both stretches of open beach and beach with fringing salt-marsh grass (*Spartina alterniflora*) beds. Those in the latter habitat do not migrate through *Spartina* after it has reached high density in June, remaining confined to the upper reaches of the beach. Numbers of *P. lapidicina* on open stretches of the beach exceed those in *Spartina* areas, and they appear to experience higher mortality in the latter area. Spiders in the low intertidal move frequently and hunt actively (cursorial strategy), those above the tideline move only 0.1 times as often and sun-bask frequently (sit-and-wait strategy). Individuals hunting in the low intertidal may capture more than one prey per day, including Diptera, Collembola, and amphipods.

Although spiders are primarily terrestrial, or sometimes occupants of the fresh water surface (Bristowe 1958; Levi 1967), several species frequent salt marshes (e.g., Teal 1962; Döbel et al. 1990) and other intertidal habitats, where they may even withstand tidal inundation (e.g., Bristowe 1923; Barnes & Barnes 1954; Roth & Brown 1976). A few even live permanently within the rocky intertidal zone, experiencing regular submersion, some for most of a tidal cycle (Hickman 1949; Lamoral 1968; McQueen & McLay 1983). Others retreat to higher sites in the vegetation as the tide encroaches (Bristowe 1958). The wolf spider *Pardosa lapidicina* Emerton 1885 (Lycosidae), the subject of this paper, exploits the intertidal span of cobble beaches in Narragansett Bay, Rhode Island, USA, moving from above the high-tide line to the low as the tide recedes, and retreating in front of its return. To the best of my knowledge, this behavior has not previously been explicitly documented in a spider. Although not tolerating submersion like a few species that frequent intertidal areas, it occupies the marine-land interface (high beach, intertidal) almost exclusively

during most of the year, using this remarkable behavior to exploit periodically available habitat. Here I document *P. lapidicina*'s abundance, distribution, movements, periodicity and prey on a cobble beach in Narragansett Bay. I then compare these results with those of other lycosids and with other reports of spiders in the intertidal zone. In particular, this analysis permits me to evaluate the hunting strategies of *Pardosa* C.L. Koch 1848, variously described as either sit-and-wait or cursorial (e.g., Bristowe 1958; Ford 1978), and rate of prey capture, frequently stated not to exceed one per day (Edgar 1970; Nyfeller & Benz 1988).

*Pardosa lapidicina* is a dark-colored wolf spider of 6-9 mm length, the females somewhat larger than the males (Kaston 1948). Mature adults weigh 30-70 mg or more, and large immatures in early September weigh 15-35 mg (Eason 1969; D.H. Morse, unpubl. data). Like other *Pardosa* (Vogel 1971; Lowrie 1973; Fujii 1974), they are small, cursorial, and nomadic. Members of the population described here, both males and females, are a uniform dull black. Voucher specimens of *P.*

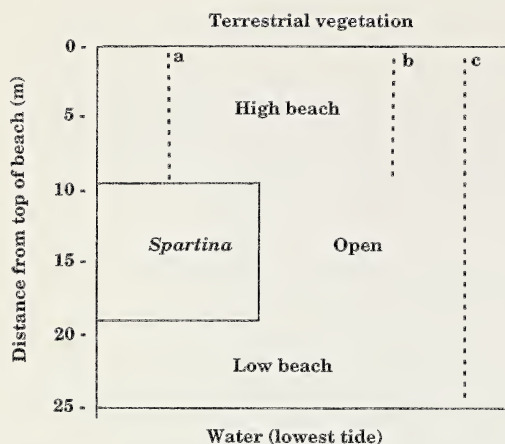


Figure 1.—Diagram of part of study area with both open cobble beach and *Spartina* areas. Transects denoted as a) high-tide census, *Spartina* area; b) high-tide census, cobble beach; and c) low-tide census, with  $0.5 \times 0.5$  quadrats, on cobble beach.

*lapidicina* have been deposited in the National Museum of Natural History, Smithsonian Institution.

### THE STUDY AREA

Spiders were studied at the Haffenreffer Estate of Brown University, Bristol, Bristol County, Rhode Island, from September 1993–September 1995. The study area is a cobble beach on the west shore of Mt. Hope Bay, a partially sheltered eastern arm of Narragansett Bay. Tides range from 0.6–2.1 m ( $\bar{x} = 1.4$  m), and the distance from the top (landward edge) of the beach only reached by severe storms to the lowest intertidal averages 23 m. Most cobbles range from 10–30 cm in diameter, and larger stones and bedrock protrude in some places. At the lower intertidal levels, some bladder wrack seaweed *Fucus vesiculosus*, as well as a variety of encrusting organisms, grow on the larger stones.

The four main study sites are cobble beaches, 30–120 m long, punctuated by fringing salt-marsh grass *Spartina alterniflora* that has invaded the beach in several places (Fig. 1). Observations and experiments were conducted on three of the beaches, with all collecting confined to the fourth, to avoid any possible effects of resulting changes in population numbers on censuses or behavior. The intervening *Spartina* areas vary between 125–150 m in length. Additionally, two narrow corridors of cobble beach (5 m, 2 m) run through

the *Spartina*. The *Spartina* areas average 7.5 m in width, and are dense, except for the landward edges. There, stem densities in the upper 50 cm range between  $0.25\text{--}0.5\times$  that of the center, which averages  $348.3 \pm 48.6$  stems/ $0.25\text{ m}^2$  ( $n = 10$ ). *Spartina* ends about 10 m from the top of the beach and 5 m above the lowest tides (Fig. 1).

A windrow of *Spartina* straw occurs high on the beach, usually 1–3 m from its upper edge. Above *Spartina*, this windrow often reaches 30 cm in height and 125 cm in width. Buildups are much less extensive on the open beach, even absent in the longest stretches. Bertness (1984) describes the study area in further detail. The land above the beach is covered by second-growth forest and scrub, with hackberry *Celtis occidentalis*, red oak *Quercus rubra*, and red cedar *Juniperus virginiana* under 20 m dominating the tree level, and bittersweet *Celastrus scandens*, greenbrier *Smilax* sp., and poison ivy *Rhus radicans* often climbing into this canopy. Other than for the vines, ground cover is sparse.

### METHODS

**Transects.**—Transects were laid out in several places on the main study sites and in *Spartina*-occupied sites between them (Fig. 1). Spiders were counted in 0.5 m wide strips centered on those lines. All rocks in these transects were moved during a census, permitting an accurate count. Two types of censuses were run. At a site on an open beach I counted spiders at low tide in  $0.5\text{ m} \times 0.5\text{ m}$  quadrats along a gradient from the top to the bottom of the beach. I ran this census weekly or biweekly over the study period, and it permitted me to assess both their numbers and distribution over the supratidal–low tidal gradient (Fig. 1c). I also counted spiders in a series of 0.5 m wide transects at high tide every other week during the second year of the study. Three areas were chosen randomly on the open beach (Fig. 1b) and three above *Spartina* regions (Fig. 1a). Six transects were run at randomly-selected sites in each of these areas, for a total of 18 transects on the open beach and 18 in the *Spartina* regions. Census methods followed those for the long-term transect described above, except that I merely counted the total in each strip, making no effort to document the position of individuals in the gradient from the top of the beach to the



water. These transects averaged 10 m or less in length, fluctuating with tidal height, and reached nearly down to the uppermost fringes of *Spartina* where it grew.

**Census at low tide.**—Spiders were also periodically counted near the low tide line, both directly between *Spartina* and the low-tide line and at the same height on open beaches. This area ranged between 2–5 m in width, depending on the daily height of the tide. During these censuses I kicked the rocks in the entire area being censused to flush spiders for counting. Efforts to calibrate this and the more time-consuming, hand-turning technique used in the transect studies indicated that “kick-sampling” yielded counts approximately half those of hand-sampling.

**Movements.**—To determine whether all individuals migrated down the open beach, I conducted a mark-and-recapture (re-sight) test. At low tide on Day 1 individuals from a stretch of 40 m along the beach were dusted with powdered micronite dye, red in the middle-low intertidal and yellow above the previous high tide. On the following day individuals were censused at both levels by kick-sampling. The one-day interval between marking and censusing assured mixing of the individuals, since spiders in the intertidal had to retreat to the supratidal during the following high tide. Two high tides thus intervened between the marking and the census, but the interval was short enough to minimize effects of molt, mortality, and recruitment. Three such markings were conducted, but inclement weather on the day following marking prevented quantitative sampling on two of these occasions.

To determine the timing of movements up and down the beach, white plastic strips 167 × 3 cm (length × width) were placed flush with the substrate, and movements of spiders across them recorded, along with their direction, over entire tidal cycles. Three strips were used simultaneously, one per observer, for a total length of 5 m.

I measured frequency of movement both in the low intertidal and high intertidal-supratidal areas of the open beach by observing focal individuals for periods of up to 30 min, since some moved only infrequently. To measure rates of movement by individuals going down and up the open beach, I timed spiders moving toward and away from the water for 10 min

periods. I remained stationary during these periods, measuring actual distances after the observations. Movements of individuals splashed by surf were measured for shorter periods of 2.0–2.5 min, the time during which they moved at high velocities.

**Distribution in winter.**—I used several methods to establish the presence and distribution of *P. lapidicina* in the forest above the beach. In September 1993, six plastic jars (9 cm diameter) were sunk into the earth flush with the surface in the scrub woodland 3 m above the beach. All were placed equidistantly along the periphery of the first beach, maintained through the fall, and their contents collected weekly. The jars were partly filled with leaves and litter to minimize possible predation and permit subsequent release. Litter above the beach was also searched for spiders between September–November 1993. Ten m<sup>2</sup> of leaf litter were turned with a coarse rake each month between May–November 1994, both at 3 m and 5–10 m above the beach.

**Activity and prey capture.**—Focal observations of spiders on the beach permitted compilation of activity patterns and time budgets. Prey capture was recorded when noted, and 10 min observation periods of individuals permitted quantification of the frequency of attacks and captures.

## RESULTS

**Population density and size.**—The weekly/biweekly transect census taken at low tide over the entire study period provided a comparison among seasons. The maximum count of spiders in this 0.5 m wide transect during late Autumn 1993 was 37 (Fig. 2). If representative of this 32 m long beach, over 2000 individuals entered winter in this one area alone. In Spring 1994, I recorded a maximum of 20 spiders, suggesting a 45% loss of individuals over the severe winter of 1993–94. Autumn counts in 1994 were only roughly half those of 1993, and those of 1995 were intermediate between those of 1993 and 1994 (Fig. 2). The cohort hatched in Spring-Summer 1994 never attained the densities of the 1993 cohort during Autumn 1993; however, their maximum numbers in Spring 1995 exceeded those from the preceding autumn (Fig. 2), suggesting low winter mortality and colonization from adjacent areas.

Numbers of adults decreased rapidly during

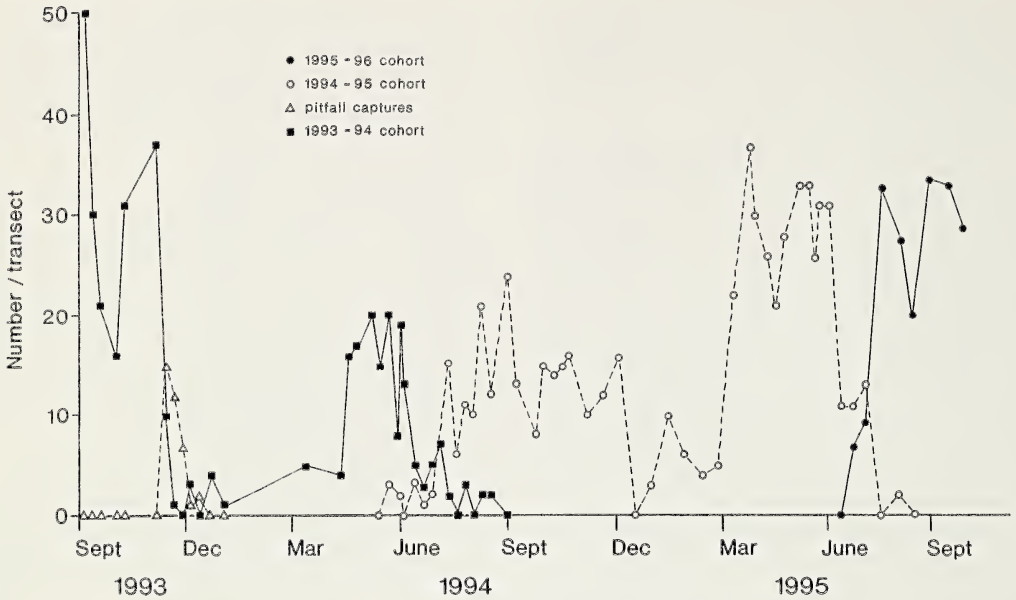


Figure 2.—Total numbers of spiders counted at low tide each 1–2 week period in 0.5 m wide transect on open beach, and numbers captured in pitfall traps.

the summer, coinciding with the appearance of young (Fig. 2), strongly suggesting that few if any individuals survived more than one year. The last adults were seen on this transect on 17 August 1994 and 1 August 1995, although occasional individuals were subsequently seen elsewhere in the study area on later dates, the last being two adults on 10 October 1994.

**Spatial distribution.**—Numbers of both adults and juveniles on bare cobble sites exceeded those on *Spartina* sites (Fig. 3,  $P = 0.01$  in a binomial test). During spring and summer, adults at bare cobble sites exceeded those at *Spartina* sites by 40% in 1994, and nearly two-fold in 1995. Differences were considerably smaller among early juveniles,

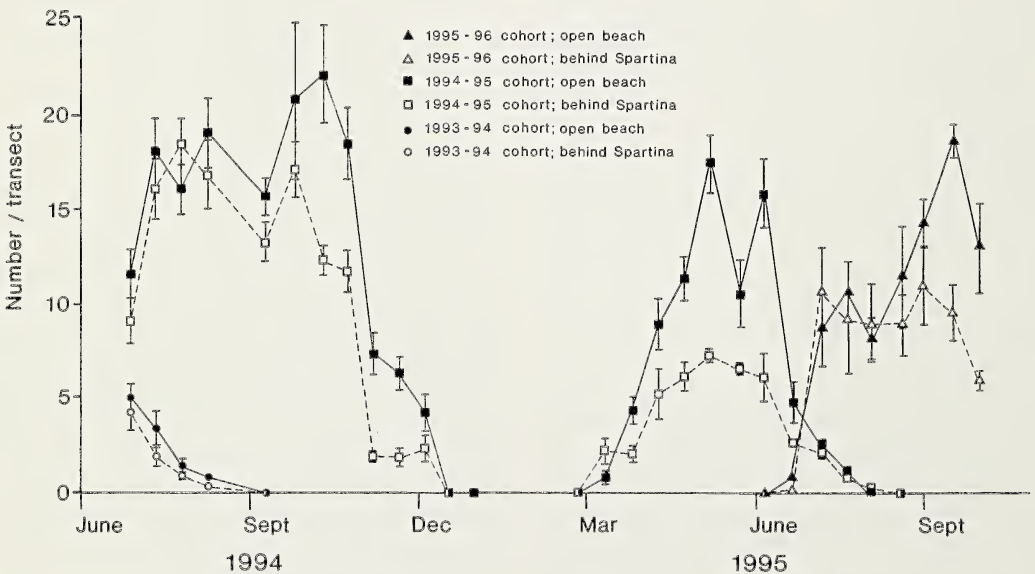


Figure 3.—Censuses at high tide in 0.5 m wide transects on open beaches and in *Spartina* areas.



Table 1.—Numbers of *Pardosa* at low tide on shoreline below *Spartina* and at same height on open beach.

Habitat	Number counts	Number of spiders	Length of shore (m)	Spiders/m
Below <i>Spartina</i>	21	0	235	0
Low open beach	8	175	295	0.6
Narrow breaks in <i>Spartina</i>	8	38	40	1.0

with numbers on the open beach averaging only 10% higher than those above *Spartina* through September 1994, before strongly diverging in late September. A similar pattern occurred in 1995, although numbers diverged by early September (Fig. 3).

*Spartina* growth generated an absolute barrier to the movement of spiders into the low intertidal area during most of the season. In six, 0.5 m wide transects made down the beach through *Spartina* in late summer, no spiders were found between the landward edge of *Spartina* and the low water line. Spiders migrating down the adjacent bare cobble beach moved no more than 8 m laterally onto the rocks below the *Spartina* fringe. At the landward edge of the *Spartina*, spiders penetrated no more than 40 cm into the vegetation. During summer and autumn I never found spiders in the low rocky areas immediately below *Spartina*, but found them common near the low-tide line on adjacent open cobble beaches (Table 1). They also readily moved through narrow corridors in *Spartina* into the low intertidal in densities comparable to or greater than those of the wider beaches (Table 1).

**Seasonal change.**—I did not find individuals in the low intertidal area after 16 October or before 17 April in the transect census, although recording them in the low intertidal during other field work as early as 25 March and as late as 20 October. Thus, the spiders confined movement into the lower reaches of the intertidal to the warmer part of the year. Even then (17 April–16 October), significantly more spiders ( $> 2.5\times$ ) occupied the high beach than the area below the wrack line in the transect ( $\chi^2 = 38.9$ ,  $df = 1$ ,  $P < 0.001$  in a  $\chi^2$  one-sample test).

In contrast, spiders moved over *Spartina*

turf before new grass sprouted in the spring, continuing while shoots were sparse and only a few cm tall (late March–late April). Numbers on the beach below *Spartina* reached 35/100 m at such times. As the grass grew taller and denser in May, only occasional spiders penetrated it ( $< 1$  vs. 20–65 individuals/100 m near the low-tide line on the open beach). No spiders were seen below *Spartina* after early June.

The movement of spiders into the adjacent forest during late fall was sudden and marked (Fig. 2). In 1993, I searched weekly for individuals under stones and in the litter within a 5 m strip above the beach, as well as monitoring six pitfall traps located 3 m above the beach. Neither the searches nor the pitfall traps yielded any spiders until 14 November 1993, when 15 individuals were captured in the pitfall traps (Fig. 2), and other individuals were found under rocks and in the vicinity of the traps. Several more individuals were captured in the traps over the following two weeks, and then captures declined to only 1–2/week, with the last individuals captured on 12 December 1993 (Fig. 2). In monthly searches of litter from May–November 1994 (0.1–10 m above beach), I found no individuals until 6 November, when I located three.

Numbers of individuals on the beach declined markedly on the first week in 1993 that spiders were captured in the pitfall traps, and in subsequent weeks only a few individuals were recorded on the beach (0–4). However, spiders occupied this site until snow and ice completely covered it on 5–6 January (Fig. 2). I also found *Pardosa* at this site on 12 March (Fig. 2), shortly after snow and ice had melted from the upper edge of the beach. Numbers of individuals on the main transect also declined during the snowless 1994–95 winter, although seldom to the level of 1993–94 (Fig. 2). However, they largely disappeared from the replicated transects (Fig. 3), suggesting that activity on the beach was confined to a few sites during the middle of the winter.

**Daily activity.**—At low tide spiders ranged over the entire vertical expanse of the open cobble during the day in dry, warm weather, although large numbers, usually a majority, occupied the supratidal part. Numbers of individuals at or above the neap high-tide line (the level at which algal wrack accumulated), about 5 m below the rock-forest interface, ex-

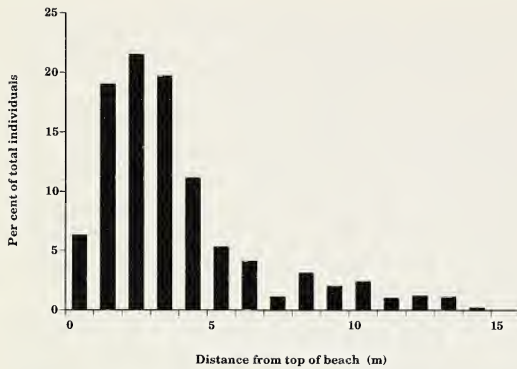


Figure 4.—Distribution of spiders at or near low tide from landward edge of beach to water. Cumulative results of  $0.5 \times 0.5$  quadrats pooled into 1 m bars. Low-tide line variable, but 15 m or more.

ceeded those below it, cumulatively over four-fold (Fig. 4:  $G = 103.6$ ,  $P < 0.001$  in a  $G$ -test,  $df = 1$ , for adults and subadults;  $G = 29.1$ ,  $P < 0.001$  in a  $G$ -test,  $df = 1$ , for juveniles), although the area below the high-tide line was often three or more times greater than the upper area.

Spiders sheltered under rocks during periods of rain and heavy overcast. After recording no individuals at the surface on three occasions (September–October 1993), I confined fieldwork to favorable weather. On two night visits during warm weather ( $> 15^\circ\text{C}$ ), all spiders were also sheltered under rocks.

Not all individuals selected the same levels of open cobble beach on subsequent days (Table 2), although significantly more were resighted at their original marking level than predicted by chance ( $Z = 1.833$ , one-tailed binomial test,  $P < 0.05$  for above the high-tide line,  $Z = 1.658$ , one-tailed binomial test,  $P < 0.05$  for the intertidal). The two groups did not differ in their tendency to shift from one level to the other on the following morning ( $G = 0.08$ ,  $df = 1$ ,  $P > 0.7$  in  $G$ -test), or in rate of recapture ( $G = 2.06$ ,  $df = 1$ ,  $P > 0.1$  in  $G$ -test). Individuals carrying egg sacs or young did not venture into the lower tidal reaches: I have yet to record such a spider over 5 m below the high-tide line.

**Movement and activity.**—Considerable numbers of individuals moved up and down the beach, the juveniles beginning in their third instars. During a representative mid-day, low-tide episode on 19 July 1994, a minimum of 26 adults and 69 young moved down and

Table 2.—Results of mark-resight test of spiders captured and marked in supratidal and low-middle intertidal areas during low tide in May 1995. Resightings made one day after marking.

Site	Number marked	Resighting same color	Resighting opposite color	Sighting unmarked
Supratidal	120	24	12	64
Low & mid-intertidal	113	28	16	71

back over a 5 m wide stretch 12.5 m below the upper edge of the beach. Extrapolated to the 120 m of this beach, over 600 adults and 1650 young moved from the high tidal to the low tidal area on that day. Spiders moved almost constantly across the counting strips, but the greatest numbers lagged the outgoing tide considerably, preceding the low tide by only 30–45 min (Fig. 5). Several even crossed downward after low tide, and a trickle of individuals continued moving downward for another 2.25 h (Fig. 5). Thus, a majority of their time in the low intertidal was spent as the tide returned toward its mid-point. Although several spiders returned only shortly before water inundated the census strip, the largest numbers preceded the resurging tide by 45–60 min (Fig. 5). Adults and young did not clearly differ in times of movement.

Movement down the beach at low tide proceeded at 17 m/h ( $2.8 \pm 1.9$  m/10 min,  $n = 10$ ), from below the wrack line to within 2 m of the water line. Return up the beach was more rapid: spiders within 5 m of the edge of the water on an advancing tide moved 42 m/h ( $n = 11$ ) ( $7.0 \pm 4.2$  m/10 min), a rate that would take them the entire breadth of the beach in under one hour. Eight individuals splashed by surf moved even faster for short periods after this stimulus (2.0–2.5 min), covering 2–3 m ( $70.9 \pm 7.8$  m/hr) over this short period. This movement consisted of several consecutive runs of up to 1 m, punctuated by rests of only a few seconds. The low variance of this sample (extremes = extrapolated rates of 60–75 m/hr) suggests that these spiders had approached their maximum possible speeds. In contrast, most upward movements of undisturbed spiders ranged between 5–50 cm ( $15.2 \pm 8.2$  cm,  $n = 17$  individuals and 182



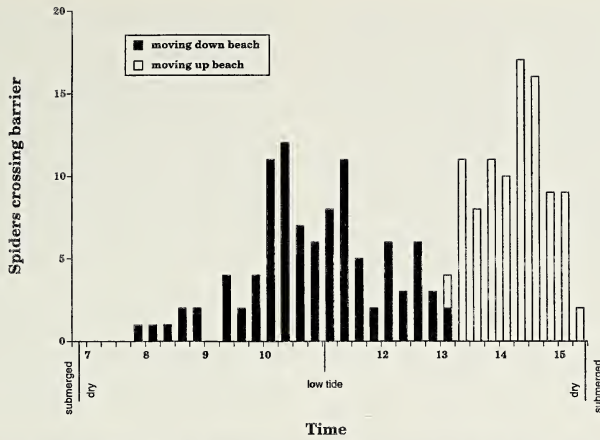


Figure 5.—Movements by spiders up and down tide line over a 5 m white plastic barrier placed 12.5 m below the upper edge of beach (mid-tide) on a routine day, 19 July 1994. Time in hours of day, period denoted as “dry” (< 0700–>1500) refers to time the barrier region was not covered with water. Adults and juveniles combined.

moves), only two moves exceeding this distance (75, 60 cm).

Spiders were significantly more active in the low intertidal than above the tide line, even when they were not migrating. Movements in the low intertidal area ( $n = 11$ ) occurred over 10 times as frequently as those in the high intertidal and supratidal ( $n = 10$ ) at the same time (every  $29.2 \pm 37.1$  sec vs. every  $412.8 \pm 624.9$  sec;  $P < 0.001$  in a two-tailed Mann Whitney  $U$ -test), a reflection of the individuals in the low intertidal being constantly on the move, often hunting, while those in the high intertidal were largely sun-basking.

Spiders usually avoided direct contact with the water, but regularly reached the water’s edge, although most frequently stopping a minimum of 0.5 m from it. Nine individuals washed into the water by unusually high waves curled their legs under them, and all

Table 3.—Prey attacked and captured by *Pardosa* on low beach, June–August (21.17 h observations). \*Spider snapped in same way as it attacked prey, but object not seen.

Prey	Attacked	Captured	Captures/h
Diptera	6	4	0.19
Collembola	10	7	0.33
Others	8	2	0.09
Not seen*	10	—	—
Total			0.52+

eventually managed to crawl out onto a nearby stone and retreat rapidly upshore ( $P = 0.004$  in a two-tailed Binomial Test). I never saw any suggestion that these spiders remained submerged during a tidal cycle.

**Prey.**—I observed 34 attacks or captures in the low intertidal, an average of 1.6/h (Table 3). Spiders attacked small flies feeding in the low intertidal (seaweed flies (*Coelopa frigida*, Coelopidae)), Collembola (*Anurida maritima*, Hypogastruridae), and unknowns, many of which probably were flies. Additionally, several apparent strikes were noted, for which the target was not seen. Probably most of these strikes were directed at Collembola (see Table 3). A majority of observed attacks directed at both the flies and Collembola was successful.

Other untimed observations on hunting and prey capture resembled these. Additionally, four captures of newly-molted amphipods (*Orchestia* sp.) warrant note. Amphipods are abundant under the rocks of the intertidal (scud, *Jassa* sp.; *Gammarus* sp.) and near the wrack line (beach fleas, *Orchestia* sp.).

DISCUSSION

**Intertidal area.**—The tide-punctuated migratory movement of *P. lapidicina* is highly unusual (or unreported). I have not found a similar pattern in the literature for any spider, although Lamoral (1968) reported that the permanently intertidal *Desis formidabilis* (O.P.-Cambridge 1890) (Desidae) from South Africa exhibited a strong sense of tidal

rhythm, remaining in their nests when tides were high at night, their normal period of activity. However, *P. lapidicina*'s behavior does somewhat resemble that of *P. pullata* (Clerck 1757), a European species Bristowe (1923, 1958). Bristowe (1958) reported them "lying idly on the pebbles piled up by the sea", but did not indicate whether they routinely moved down into the intertidal as *P. lapidicina* does. However, he noted that these *P. pullata* retreated up the tide line into vegetation when exceptionally high tides occurred, but were occasionally trapped by these tides. If so trapped, they curled their legs under them, as does *P. lapidicina*, and floated passively on the wave until it receded, depositing them on the pebble substrate. Then they ran toward the land before the next wave arrived, and similarly to *P. lapidicina*, always succeeded in escaping.

*Pardosa lapidicina* is common enough to play an important energetic role in the intertidal zone. Such a role would not be unusual, since spiders, especially lycosids, are the dominant invertebrate predators in some streamside (Vlijm et al. 1963), salt-marsh (Schaefer 1974), grassland (Van Hook 1971) and forest habitats (Moulder & Reichle 1972).

**Effect of *Spartina* barriers.**—Spiders of the open beach appeared to be more successful than those in the *Spartina* areas. Densities were almost always higher on the open beach, although differences were initially small in the immature cohort during mid-summer. However, the rapid decrease in numbers of spiders in the *Spartina* areas during the fall suggests lower survival there than on the open beaches. Spiders in the *Spartina* areas may have been in poorer energetic condition than those from the open beach.

**Activity.**—The behavior of individuals in supratidal and intertidal areas differed markedly. In the supratidal area, spiders moved relatively infrequently and often sunbasked. Their behavior resembled that of several other *Pardosa* species, which employ sit-and-wait behavior almost exclusively, waiting until prey come very close to them (Edgar 1969; Kronk & Riechert 1979; Nakamura 1982) or even touch them (Fujii 1974; Ford 1978), only then rapidly attacking. Traditionally, lycosids, including *Pardosa*, have been considered cursorial predators that tracked down their prey

(e.g., Comstock 1940; Bristowe 1958), and the previously-noted authors go to considerable ends to "correct" the record. Ford (1978) noted that his *P. amentata* (Clerck 1757) spent no more than 278 sec/day moving (0.0032%/day). The *P. lapidicina* in the supratidal and high intertidal areas exhibited a sit-and-wait pattern closely resembling the one described by the more recent workers, which simultaneously allowed them to sun-bask on clear days. Those on the low beach, however, moved much more frequently, often stalking and leaping at flies, active behavior similar to that described by Bristowe and other earlier workers. In light of these striking differences and the disagreement in the literature, detailed time budgets of a representative range of species are needed.

The high rates of movement observed in wave-splashed spiders resembled the maximum movement rates of both *P. lugubris* (Walckenaer 1802) and *Xerolycosa nemoralis* (Westring 1861) continually chased by Bristowe (1939), who found that they could run a maximum of 1.8 and 1.5 m, respectively, before experiencing temporary exhaustion. These figures appear comparable to the rapid moves of 2–3 m seen in bursts of up to 1 m by *P. lapidicina* not subjected to these artificial stimuli.

**Hunting.**—Studies of lycosids in the field reveal very low percentages of individuals found feeding on prey (2% -Nakamura 1982; 6% -Nyffeler & Benz 1981a), consistent with a low intake rate. Some lycosids are estimated to capture no more than one prey per day in the field (Edgar 1970; Nyffeler & Benz 1988), although they routinely accept several per day in the laboratory (Miyashita 1968; Samu 1993). Observations in this study suggested that individuals in the low intertidal area routinely captured more than one prey per day; however, many of those prey were tiny collembolans, which provide only a minute store of resources. Although amphipods are abundant on the beach, they typically have hard carapaces and hence may be difficult to procure (Moulder & Reichle 1972), unless they have recently molted. All amphipod prey in this study had recently molted. Other small lycosids also take small prey (Fitch 1963; Dondale et al. 1972; Nyffeler & Benz 1981a, 1981b) and experience considerable difficulty



taking any with a hard carapace (Moulder & Reichle 1972).

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## NOTES ON THE REPRODUCTIVE BIOLOGY AND SOCIAL BEHAVIOR OF TWO SYMPATRIC SPECIES OF *PHILOPONELLA* (ARANEAE, ULOBORIDAE)

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**ABSTRACT.** Populations of the facultatively communal species *Philoponella oweni* (Chamberlin 1924) and *Philoponella arizonica* (Gertsch 1936) (Uloboridae) occur sympatrically in the Chiricahua mountains of southeastern Arizona. This study compares reproductive biology, structure of communal groups, and feeding rates of the two species, and documents differences in their phenology, webs, web construction sites, egg-cases and spiderlings. I suggest environmental factors that may select for different reproductive strategies in the two species.

Many members of the spider family Uloboridae have been observed living in groups (Opell 1979; Muma & Gertsch 1964). For only a few of these species has the nature of their group-living behavior been investigated: the facultatively communal *Philoponella oweni* (see Smith 1982, 1983) and *P. semiplumosa* (Simon 1893)(see Lahmann & Eberhard 1979); *P. republicana* (Simon 1891), with its large, semi-permanent colonies (Smith 1985; Binford & Rypstra 1992); and a west African *Philoponella* Mello-Leitão which was observed in a very large colony (Breitwisch 1989).

This study compares reproductive biology, feeding rates and group-living behavior of two sympatric populations of group-living *Philoponella*, *P. oweni* (Chamberlin) and *P. arizonica* (Gertsch) (Uloboridae). Notes on the natural history of the two species are also presented, including structure of the egg-cases, the structure of the webs and substrates used for web-building in the two species.

Populations of *Philoponella oweni* and *P. arizonica* are broadly sympatric in the southwestern United States and northeastern Mexico (Muma & Gertsch 1964; Opell 1979). The basic life cycles of the two species are similar in southeastern Arizona. Field observations indicate that both are annual; sub-adults emerge from overwintering sites in the spring (early April to early June, depending on elevation). Mating takes place in late spring and early summer. In general, males are shorter-

lived than females and disappear from the population during the course of the summer. Females can lay eggs throughout the summer and may survive until early autumn, but in the populations studied no adult females overwintered for a second breeding season.

Immatures hatch and emerge from the egg-case during the summer. As is true of other uloborid spiders, the young can spin webs in the first post-emergence instar (Szlep 1961; Eberhard 1977). The newly emerged spiderlings lack a functional cribellum; and the orb webs they produce are distinctive, containing many hundreds of radial threads without a sticky spiral. Later instars possess a functional cribellum and produce webs that are similar or identical to those of adults in form (Szlep 1961; Eberhard 1977).

The young remain with the female for a variable length of time and attach their orbs to her web; during the course of the summer some or all of them disperse out of the maternal web and build independent webs (Smith 1982). Young spiders over-winter as sub-adults or younger immatures, and emerge the following spring to form the next generation of reproductives.

Both species are facultatively communal; that is, adult females of both species can be found living in small communal groups or as solitary individuals (Smith 1982, 1983). In the communal groups each female constructs her own orb web and defends it against other adult females. The orbs are joined by their support lines and space webbing.



Figure 1.—Egg-cases of *Philoponella oweni* (above) and *Philoponella arizonica* (below).

Both species suffer from egg-parasitism by the chalcidoid wasp *Arachnopteromalus dasys* Gordh (Pteromalidae) (Gordh 1976), which greatly affects reproductive success of individual females. The female wasp oviposits in a uloborid spider's egg-case, and the larvae consume the contents of the spider's eggs, leaving behind empty spider egg shells. The wasp larvae then pupate inside the spider egg-case and emerge as adults. If an egg-case is parasitized, all of the spider eggs inside are killed (Smith 1982).

### METHODS

Observations and collections were made at several sites in the Chiricahua Mountains in southeastern Arizona: the Southwestern Research Station of the American Museum of Natural History; South Fork Canyon, Cave Creek Canyon, and Herb Martyr Reservoir in the Coronado National Forest; and the town of Portal (Cochise County).

**Population censuses:** Adult females and some males were individually color-marked with dots of fast-drying enamel paints (Testor's model airplane paint) and censused 2–5 times per week. From 25 April–20 August 1977 I censused a marked population of *P. oweni* in Cave Creek Canyon at an elevation of approximately 1695 m. This population was destroyed by a flood in 1978. From 3 June–18 September 1979 I censused marked populations of *P. oweni* and *P. arizonica* in South Fork Canyon. The *P. arizonica* population was located in the lower part of the canyon (1525–1660 m) while the *P. oweni* population was in the upper part of the canyon (1630–1730 m). At each census visit I noted the presence of adult females, males, immatures or egg-cases.

**Reproductive biology:** When a female produced an egg-case it was given a color mark corresponding to that of the mother. To determine mean clutch size (number of eggs per egg-case) for each species I collected the egg-cases after the young had emerged and examined their contents with a dissecting microscope. As is true of most spiders, the young of *Philoponella* do not emerge from the egg-case immediately upon hatching from the egg; they remain in the egg-case for one instar, molt, and emerge as second instar spiderlings leaving behind both empty egg-shells and cast-off exoskeletons. In healthy egg-cases I used the number of egg shells as a measure of the number of eggs laid in the egg-case (Smith 1982). A parasitized egg-case can be recognized by the absence of exoskeletons from first instar spiderlings and presence of wasp pupal skins. Although all the spider eggs are killed in a parasitized egg-case, the egg-shells are still visible and were used to infer the original clutch size.

**Colony structure:** I noted the size and organization of all communal groups formed by each species in several locations: *P. oweni* in Cave Creek Canyon (1977), South Fork Canyon (1979, 1980) and Herb Martyr (1980); *P. arizonica* in South Fork Canyon (1979, 1980).

**Feeding rates:** From 21–27 August 1979, I compared feeding rates of solitary and communal females of the two species in South Fork Canyon using a trapline census method. Censuses were carried out from 0600–1800 h. Daily census periods were 4–6 h long, for a total of 29 h of observation. Every hour I visited each female in the study area and recorded whether or not she was feeding or engaged in prey capture.

**Web structure:** In July and August of 1980 I measured the webs of all adult females found in the South Fork Canyon study area: 22 webs of *P. oweni* and 19 webs of *P. arizonica*. I measured longest diameter of the orb webs and deviation (to the nearest 10°) of the plane of the orb webs from horizontal, and counted number of radii and number of spiral turns along the longest radius. I also noted the amount and position of "space webbing" (irregular tangles of threads), the presence or absence of a stabilimentum and the general appearance of the webs.

**Habitat:** To evaluate the distribution of the two species with respect to elevation I located



Table 1.—Phenological data for *Philoponella oweni* and *Philoponella arizonica*. \* Still active when field observations ended.

	<i>oweni</i> (1977) Cave Creek	<i>oweni</i> (1979) South Fork	<i>arizonica</i> (1979) South Fork
Date census began	26 April	3 June	3 June
First adult female seen	5 May	3 June	3 July
First adult male seen	5 May	3 June	3 July
First egg-case seen	16 June	12 June	3 July
First hatchlings seen	28 June	2 July	5 July
Last adult male	4 July	27 June	21 July
Last adult female	20 August*	11 July	18 September*
End of census	20 August	18 September	18 September

all collection sites (eight for *P. oweni*, six for *P. arizonica*) on a topographical map. I also recorded the substrates used for web attachment by members of each species. In July and August 1977 I recorded the substrates used for 25 *P. oweni* webs in Cave Creek Canyon, and in August 1979 I recorded the substrates of 36 *P. oweni* and 31 *P. arizonica* webs in South Fork Canyon (in each case, this represented all adult webs present in the study sites).

*Egg-cases:* In July 1980 I collected 24 empty *P. oweni* egg-cases and 33 empty *P. arizonica* egg-cases and measured maximum width and length to the nearest mm using dial calipers, and noted their color, shape and ornamentation.

RESULTS

*Population censuses:* Table 1 gives the dates of first sightings of age and sex classes of both species. These data are limited by the starting and finishing dates of the censuses, but still show differences between adjacent populations of *P. oweni* and *arizonica*. *P. oweni* adults appear sooner (at a given altitude) and adult *P. oweni* males disappear from these populations by late June and early July. Adults of *P. arizonica* appear later, and the adult males persist in populations until late July. There was little temporal overlap between *P. oweni* males and *P. arizonica* females in adjacent populations.

*Reproductive biology:* Table 2 presents data on reproductive parameters for all females in the study areas, whether or not complete records of their reproductive history could be made. In 1979 I had complete reproductive histories for 31 *P. oweni* females and 25 *P. arizonica* females. These data are presented in

Table 3. Both tables show that *P. oweni* females produce fewer egg-cases per female and lay more eggs per egg-case than do *P. arizonica* females. The behavior of females with egg-cases also differs between the two species.

A female *P. oweni* about to construct an egg-case leaves her prey-capture orb and moves to the retreat area, a protected area near the orb usually under a rock or log, and constructs the egg-case there. There she remains, holding the egg-case and (presumably feeding little or not at all) until the young emerge, a period of approximately 20 days. After the young emerge the mother discards the egg-case, leaves the retreat, and spins a new prey capture-orb. *P. oweni* females usually have one or at most two egg-cases at a time. The time interval between successive egg-cases produced by a female is more than a week, typically 2–3 weeks.

In contrast, females of *P. arizonica* were never seen to leave the orb with their egg-cases. These females suspend their spindle-shaped egg-cases from the hub of their horizontal orbs. As new egg-cases are constructed, at intervals of 4–10 days, they are attached to the egg-cases already hanging in the web to form a long, slender stick (Fig. 1). The female continues feeding while the eggs and young mature. *P. arizonica* females sometimes have as many as 8 egg-cases in the web at once. Egg-case parasitism by the wasp *A. dasys* (Fig. 2) is a major source of mortality in both species. In general, a higher proportion of the egg-cases of *P. arizonica* than of *P. oweni* are attacked by egg-case parasites. In 1979, 14% of the egg-cases produced by *P. oweni* females and 27% of the egg-cases pro-

Table 2.—Reproductive parameters for *Philoponella oweni* and *Philoponella arizonica*, Cave Creek Canyon in 1977 and South Fork Canyon in 1979. Statistical tests are for differences between adjacent *Philoponella oweni* and *Philoponella arizonica* populations in South Fork Canyon in 1979. <sup>a</sup> = Mann Whitney *U*-test; <sup>b</sup> = two-tailed *t*-test for samples with equal variance, *t* = 13.5; <sup>c</sup>,  $\chi^2$  = 3.21, 1 *df*; <sup>d</sup>,  $\chi^2$  = 7.10, 1 *df*; <sup>e</sup>, Mann Whitney *U*-test.

		Year	Mean	SD	Range	<i>n</i>	<i>P</i>
Egg-cases per female	<i>oweni</i>	1977	1.29	0.50	1–3	49 females	
	<i>oweni</i>	1979	1.5	10.8	1–4	44	<0.001 <sup>a</sup>
	<i>arizonica</i>	1979	3.2	2.0	1–8	50	
Clutch size	<i>oweni</i>	1977	35.2	15.6	10–85	51 egg-cases	
	<i>oweni</i>	1979	50.0	17.0	14–89	50	<0.001 <sup>b</sup>
	<i>arizonica</i>	1979	21.8	8.9	6–49	112	
Egg-cases parasitized	<i>oweni</i>	1977	23.5%			51 egg-cases	
	<i>oweni</i>	1979	14.0%			50	0.073 <sup>c</sup>
	<i>arizonica</i>	1979	27.0%			112	
Females with ≥ 1 egg-case parasitized	<i>oweni</i>	1977	40.0%			30 females	
	<i>oweni</i>	1979	22.0%			32	<0.007 <sup>d</sup>
	<i>arizonica</i>	1979	55.0%			27	
Live young per egg-case	<i>oweni</i>	1977	27.1	20.1	0–79	51 egg-cases	
	<i>oweni</i>	1979	42.5	21.5	0–88	50	<0.001 <sup>e</sup>
	<i>arizonica</i>	1979	15.8	12.0	0–41	112	

duced by *P. arizonica* females were parasitized (this difference is not significant;  $\chi^2$  = 3.21, 1 *df*, Table 2). For females for whom complete reproductive histories were recorded (Table 3), significantly more egg-cases of *P. arizonica* than of *P. oweni* were parasitized. Similarly, for all females and for females with complete reproductive records, a higher proportion of *P. arizonica* females than *P. oweni* females lost at least one egg-case to parasites. Because the average clutch size of *P. oweni* females is larger than that of *P. arizonica* females, the appropriate comparison of reproductive effort and reproductive success is lifetime egg and spiderling production of

individual females (Table 3). Mean lifetime egg production by *P. oweni* and *arizonica* females did not differ significantly, nor did mean lifetime production of live spiderlings (Mann Whitney *U*-test). However, 19% of *P. oweni* females (6 of 31) lost all of their eggs to parasites, while only 4% of the *P. arizonica* females (1 of 25) was similarly affected. While this difference is not significant ( $\chi^2$  = 2.9, 1 *df*), it does suggest that *P. arizonica*'s habit of packaging lifetime egg production into many small clutches may reduce the risk of losing an entire lifetime of egg production to parasites. A comparison can also be made between

Table 3.—Lifetime reproductive parameters for *Philoponella oweni* and *P. arizonica* for whom complete life histories are known (South Fork Canyon, 1979). <sup>a</sup> = Mann Whitney *U*-test; <sup>b</sup> = two-tailed *t*-test for samples with equal variance, *t* = -1.73; <sup>c</sup>  $\chi^2$  = 18.16, 1 *df*; <sup>d</sup>,  $\chi^2$  = 8.16, 1 *df*; <sup>e</sup>, Mann Whitney *U*-test.

		Mean	SD	Median	Range	<i>n</i>	<i>P</i>
Egg-cases per female	<i>oweni</i>	1.3	0.5	1.0	1–2	31 females	<0.001 <sup>a</sup>
	<i>arizonica</i>	3.9	1.9	4.0	1–8	25	
Total eggs	<i>oweni</i>	66.3	21.4	68.0	30–100	31 females	0.09 <sup>b</sup> (ns)
	<i>arizonica</i>	82.4	42.3	76.0	17–208	25	
Egg-cases parasitized	<i>oweni</i>	15.0%				40 egg-cases	0.00002 <sup>c</sup>
	<i>arizonica</i>	54.0%				97	
Females with ≥ 1 egg-case parasitized	<i>oweni</i>	16%				31 females	0.0043 <sup>d</sup>
	<i>arizonica</i>	52%				25	
Total young	<i>oweni</i>	54.8	32.7	62.0	0–100	31 females	0.91 <sup>e</sup> (ns)
	<i>arizonica</i>	58.0	36.2	55.0	0–159	25	





Figure 2.—*Arachnapteromalus dasys* on *Philoponella oweni* egg-cases.

the solitary and group-living members of each species. It was reported earlier (Smith 1982) that on average, communal females *P. oweni* produced more eggs per egg case than solitary females, though they did not differ in mean number of egg cases per female (1977: solitary females,  $26.9 \pm 13$  eggs per egg case,  $n = 13$  cases; communal females,  $37.3 \pm 15.1$  eggs per egg case,  $n = 38$  egg cases,  $t = 2.17$ ,  $P < 0.05$ . 1979: solitary females  $44.3 \pm 15.3$  eggs,  $n = 26$  cases; communal females  $56.1 \pm 17.0$  eggs,  $n = 24$  cases,  $t = 2.57$ ,  $P < 0.05$ ).

In *P. arizonica*, no difference was observed in the number of eggs per egg case produced by solitary and communal females: solitary females,  $21.5 \pm 9.1$  eggs per egg case,  $n = 69$  cases; communal females,  $22.2 \pm 8.61$  eggs,  $n = 42$  cases. Because females in this species make a large number of egg cases, it is difficult to be sure all egg cases are noted and collected; thus estimating the mean number of egg cases per female is difficult. Given these caveats, there does not appear to be any significant difference in number of egg cases per female. For all females, the mean number of (observed) egg cases per female was  $2.35 \pm 1.9$  for solitary females ( $n = 40$  females),  $2.6 \pm 2.7$  for communal females ( $n = 25$  females;  $t = 0.44$ ,  $P < 0.66$ , 63 *df*, two-tailed test, equal variances). For those females ob-

served with at least one egg case, the figures are  $2.9 \pm 1.6$  egg cases per solitary female ( $n = 32$  females),  $3.61 \pm 2.5$  per communal female ( $n = 18$  females;  $t = 1.15$ ,  $P < 0.26$ , 48 *df*).

**Colony structure:** Both species occur in solitary webs and in aggregations. The aggregations of both species contain two or more adult females, each with her own prey capture orb. The aggregations formed by the two species differ in several respects.

Colonies of *P. oweni* attained larger size than those of *P. arizonica*: the largest *P. oweni* colony observed contained 44 adult females plus males and immatures. The mean number of females per web site at various locations were: Cave Creek Canyon 1977,  $3.5 \pm 8.6$  (range 1–44,  $n = 25$  web sites, 87 ♀); South Fork Canyon, 1979,  $1.7 \pm 2.0$  (range 1–11,  $n = 52$  web sites, 87 ♀); and Herb Martyr, 1979,  $1.3 \pm 0.6$  (range 1–4,  $n = 40$  web sites, 53 ♀).

In *P. oweni* colonies, orbs of adults and immatures share support lines. The orbs are arranged side by side in loose sheets of orbs, and several orbs or sheets of orbs may be stacked one over the other. Retreat(s) are not specially constructed by colony members; they are simply protected areas near the web such as a cleft under a rock or log surrounded by old webbing. The retreat or retreats may be used in common by all colony members.

Aggregations of *P. arizonica* are smaller and simpler. The largest aggregation ever observed (in 1980) contained eight adult females. In 1979 the mean number of females/web site in South Fork Canyon was:  $1.7 \pm 1.2$  (range 1–6,  $n = 45$  web sites, 76 ♀). Males and immatures may also be present in aggregations. The webs in an aggregation are side by side, joined by their space webbing. Retreats are usually absent.

**Feeding rates:** Females of *P. oweni* spent a greater proportion of time feeding during the census period. On average  $41.7 \pm 17.8\%$  of *P. oweni* females and  $26.5 \pm 11.7\%$  of *P. arizonica* females were feeding per census hour (29 h, 10–13 *P. oweni* females, 17–20 *P. arizonica* females,  $P = 0.0009$ , Mann Whitney *U*-test). These measurements can be broken down to compare the feeding rates of solitary and aggregated females. In *P. oweni* an average of  $53.1 \pm 22.9\%$  of communal females were feeding per census hour (6–8 fe-

Table 4.—Web measurements for *Philoponella oweni* and *Philoponella arizonica*;  $n = 22$  webs of adult female *Philoponella oweni*, 19 webs of adult female *P. arizonica*. (Significance determined by two-tailed  $t$ -test for samples with equal variance).

Parameter		Mean	SD	$P$
Longest diameter	<i>oweni</i>	27.8 cm	10.6	<0.001
	<i>arizonica</i>	12.4	3.8	
Number of radii	<i>oweni</i>	27.9	7.0	>0.05
	<i>arizonica</i>	29.2	9.0	
Number of spiral turns	<i>oweni</i>	25.6	10.5	<0.005
	<i>arizonica</i>	16.4	8.4	
Deviation from horizontal	<i>oweni</i>	51.9°	24.2	<0.001
	<i>arizonica</i>	6.8°	13.8	
Stabilimentum present	<i>oweni</i>	73%		
	<i>arizonica</i>	0%		

males). This is significantly more than the time spent feeding by any other class of females (29 h,  $P = 0.001$  or less, Mann Whitney  $U$ -test). There was no significant difference among the other three classes ( $P = 0.40$  or more, Mann Whitney  $U$ -test): solitary *P. oweni*,  $22.9 \pm \text{SD } 22.2\%$  females feeding per hour,  $n = 2\text{--}5$  females; aggregated *P. arizonica*,  $28.7 \pm \text{SD } 15.7\%$  females feeding per hour,  $n = 7\text{--}10$  females; solitary *P. arizonica*,  $25.2 \pm \text{SD } 15.4\%$  feeding per hour,  $n = 7\text{--}11$  females.

**Web structure:** Web measurements are presented in Table 4. Female *P. oweni* construct relatively large orbs which are closer to vertical than horizontal. There is a small quantity of space webbing below and around the orb, but there is seldom any above the orb. Stabilimenta are usually present. The web *P. arizonica* consists of a small horizontal orb surrounded above, below and around the edges with space webbing. The orb is sometimes drawn up in the center by threads attached to

the hub, giving it a slightly domed appearance. In many orbs the radials are not all in one plane, giving the orb a pleated appearance. None of these webs had stabilimenta.

**Habitats:** In August 1980 all populations of *P. oweni* sampled were found at an elevation of 1630 m or higher (1630–1950 m) while all populations of *P. arizonica* were below 1630 m (1460–1630 m). The *P. oweni* webs were usually built in protected locations such as hollow trees and clefts between rocks. The *P. arizonica* webs were built in more open areas, such as in brush, shrubs or grass (Table 5).

**Egg-cases and immatures:** The two species differ in the structure of their egg-cases. *Philoponella oweni* constructs large beige or cocoa-colored stellate egg-cases which are more-or-less flat on one side and domed on the other (Fig. 1). The mean length of the 24 egg cases measured was 6.7 mm (SD  $\pm 0.96$ , range 5.2–5.8 mm); mean width was 4.4 mm (SD  $\pm 0.61$ , range 2.9–5.4 mm). These cases are heavily decorated with small spikes of

Table 5.—Substrates used for web construction by *Philoponella oweni* and *Philoponella arizonica*: 1977, Cave Creek population; 1979, South Fork Canyon populations. <sup>a</sup> *Yucca schottii* absent from site.

			Rocks	<i>Yucca schottii</i>	Brush, shrubs	Herbs, grass	Base of trees	Along logs	Hollow trees	Total
1977	<i>oweni</i>	$n$	10	<sup>a</sup>	0	0	6	6	3	25
		%	40		0	0	24	24	12	100
1979	<i>oweni</i>	$n$	18	0	6	1	3	4	1	36
		%	50	0	17	3	8	11	3	100
1979	<i>arizonica</i>	$n$	3	15	6	6	1	0	0	31
		%	10	48	19	19	3	0	0	100



silk, especially on the curved side (spikes on flat side: median 5, range 0–22; spikes on curved side: median 13, range 5–24). *Philoponella arizonica* constructs pale smooth, whitish or bone colored egg-cases (Fig. 1). These cases are spindle-shaped, and there are usually no decorations or projections (of 33 egg-cases only eight were decorated with spikes, ranging in number from 7–12). Mean length of the 33 egg cases measured was 7.4 mm (SD  $\pm$  1.1, range 5.1–9.1 mm); mean width was 2.8 mm (SD  $\pm$  0.30, range 2.2–3.4 mm).

The immatures of the two species are also recognizably different. *P. oweni* immatures are black with white markings and *P. arizonica* immatures are yellow with brown markings.

### DISCUSSION

*Philoponella oweni* and *P. arizonica* are found in close proximity in both time and space and occupy similar habitats. Although they are similar in appearance, they can easily be distinguished in the field by structure of the orb webs, nature of the communal groups (where they exist), the form of the egg cases and the coloration of second instar spiderlings. They also tend to use different substrates for web construction, with *P. oweni* making use of rigid substrates such as fallen logs, hollow trees, and niches under rocks, and *P. arizonica* making greater use of vegetation such as shrubs, grasses and yuccas as substrate.

An enhanced food supply (whether due to higher prey capture rate, reduced prey handling time, increased size of prey, or other factors) has often been proposed as a benefit of group-living behavior in spiders (e.g., Binford & Rypstra 1992, Buskirk 1975, 1981; Nentwig 1985; Rypstra 1979, 1990). This study showed an interesting difference in feeding rates of the solitary and communal females *P. oweni* and *P. arizonica*. As was reported earlier (Smith 1983), among *P. oweni* the proportion of females feeding per hour was greater for communal than for solitary females. Insect trapping at the sites of communal and solitary *P. oweni* webs indicated that insect abundance was greater at sites occupied by colonies than at sites occupied by single webs. This suggests that communal groups are feasible at sites where insect abundance is high enough to support several females.

Among *P. arizonica*, there was no difference in the feeding rates of solitary and communal females—both were similar to the feeding rates of solitary *P. oweni*. No insect trapping was done in the vicinity of *P. arizonica* colonies and solitary webs, so it is not possible to say if insect abundance differs between the sites of colonies and solitary webs.

The earlier report on communal behavior of *P. oweni* also showed that females in communal groups produced a greater number of eggs per egg case than did solitary females, though total live young per female was the same for the two groups due to higher rates of egg case parasitism in the communal groups (Smith 1982). One explanation for this difference could be the difference in feeding rates between solitary and communal females. We observed no significant difference between solitary and communal *P. arizonica* either in number of eggs per egg case or in egg cases per female, which dovetails with the feeding rates observed. However, as noted above, there are problems in collecting data on the number of egg cases per female in this species. Additional comparative study of the reproductive biology of communal and solitary *Philoponella* is warranted.

Over their lifetimes, females of the two species produce the same average number of eggs and the same number of live second instar spiderlings. However the two species differ in the way they package their eggs and care for the egg cases. *P. oweni* females package their eggs in one or a few large packets and make what appears to be a large expenditure in parental care, in the form of guarding the egg-case without feeding. The females of *P. arizonica*, on the other hand, package their eggs into many small packets and continue to feed in their orbs while the egg-cases are suspended in the web.

Both species are subject to the same egg parasite, *Arachnopteromalus dasys*. It is not clear if the different egg-case tending behaviors of *P. oweni* and *P. arizonica* have any effect against egg parasites such as *Arachnopteromalus dasys*. One might suppose that the behavior of *P. oweni* affords more protection than that of *P. arizonica*. However another uloborid spider, *Uloborus glomosus* (Walckenaer 1841), also makes several small-egg cases which it attaches to the web. In this species, the female has been observed to jerk the



web and make leg sweeping motions in response to parasitoid wasps (and spiderlings) crawling on the egg-cases (Cushing 1989; Cushing & Opell 1990), though it is not clear how effective this is in deterring parasites. I have observed *A. dasys* crawling on the egg-cases of both *P. oweni* and *P. arizonica* with no obvious reaction from the mothers of eggs.

It is possible to make some testable hypotheses concerning the adaptive significance (or lack of it) of the *Philoponella* egg-case tending behaviors. These hypotheses fall into four categories: those dealing with uncertainties faced by the female, those dealing with uncertainties faced by the young, those which consider differences in clutch size as side-effects of other maternal behaviors, and non-adaptive explanations.

*Hypothesis 1:* *P. arizonica* females face more uncertainties in food supply than *P. oweni* females. When they gather enough resources for a small batch of eggs they produce a clutch right away; if they were to wait for additional prey they might use up their small reserve of energy in maintenance activities. This can be tested by measuring the feeding rates of marked individuals over time. *P. arizonica* females would be expected to have a higher variance in feeding rate than *P. oweni* females.

*Hypothesis 2:* *P. arizonica* females are subject to a high and constant probability of mortality over their adult lives, while *P. oweni* females have relatively low probability dying before the first clutch is laid. It doesn't pay a *P. arizonica* female to save up resources for a large clutch if there is a good chance she will die before it can be laid. Life history data, particularly from the early part of the breeding season, are needed to test this hypothesis.

*Hypothesis 3:* Females of *P. oweni* must guard their egg-cases because predators and egg-parasites are more common in their environment than in that of *P. arizonica*. It would be more economical to produce a single large clutch than many small ones, since it takes as much time and energy to guard a small egg-case as a large one. This assumes that the type of maternal care shown by the bag species actually is more effective than that of the *P. arizonica* females in preventing parasitism or predation. This can be tested by removing females from egg-cases, leaving the egg-cases *in situ*, and comparing the rates of

parasitism on unguarded *P. arizonica* and *P. oweni* egg-cases to rates of parasitism on unmanipulated egg-cases.

*Hypothesis 4:* *P. arizonica* is subject to a risky, unpredictable environment. The *P. arizonica* pattern of reproduction ensures that at least some of a female's offspring may hatch at a time when conditions are favorable. One obvious possibility is that spiderlings require a supply of very small prey, and that the availability of these insects varies unpredictably over time. Little is known about the feeding behavior and survivorship of spiderlings. A first step would be to examine feeding behavior and prey of hatchlings, record variation in juvenile feeding rates over time, and correlate fluctuations in feeding rate with fluctuations in environmental factors such as rainfall.

*Hypothesis 5:* The differences in reproductive behaviors are not adaptations to any differences in ecology, behavior or microhabitat. Each species is conservative in behavior and displays the maternal behavior typical of its closest relatives. The first step in testing this hypothesis would be to construct a phylogeny for species in the *Philoponella semiplumosa* species group (Opell 1979, 1987), and examine the maternal behavior of the closest relatives of *P. oweni* and *P. arizonica* species.

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## BEHAVIOR AND NICHE SELECTION BY MAILBOX SPIDERS

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**ABSTRACT.** The data for species of spiders observed and collected for a period of eight years from a rural delivery mailbox route in Mashpee, Massachusetts is examined. We collected 1252 individuals, with 199 species represented. Some species were year-round residents of mailboxes while others appeared only during limited periods of time. Species typically found in the foliage of coniferous trees and on the trunks of pines and oaks dominated the collections, with lesser numbers from other types of habitats. The species observed are divided into categories depending upon their consistency in terms of time of occurrence and number. Species that occurred only rarely tended to be different from year to year.

Arachnologists have long been aware that the structure of the habitat, along with seasonal and other environmental factors, plays a dominant role in determining where spiders are to be found (Stratton, Uetz & Dillery 1978; Hatley & MacMahon 1980; Bultman & Uetz 1983; Gunnarsson 1983, 1992; Greenstone 1984; Rypstra 1986; Moring & Stewart 1994; Reichert & Gillespie 1986; Rushton 1991; Sundberg & Gunnarsson 1994).

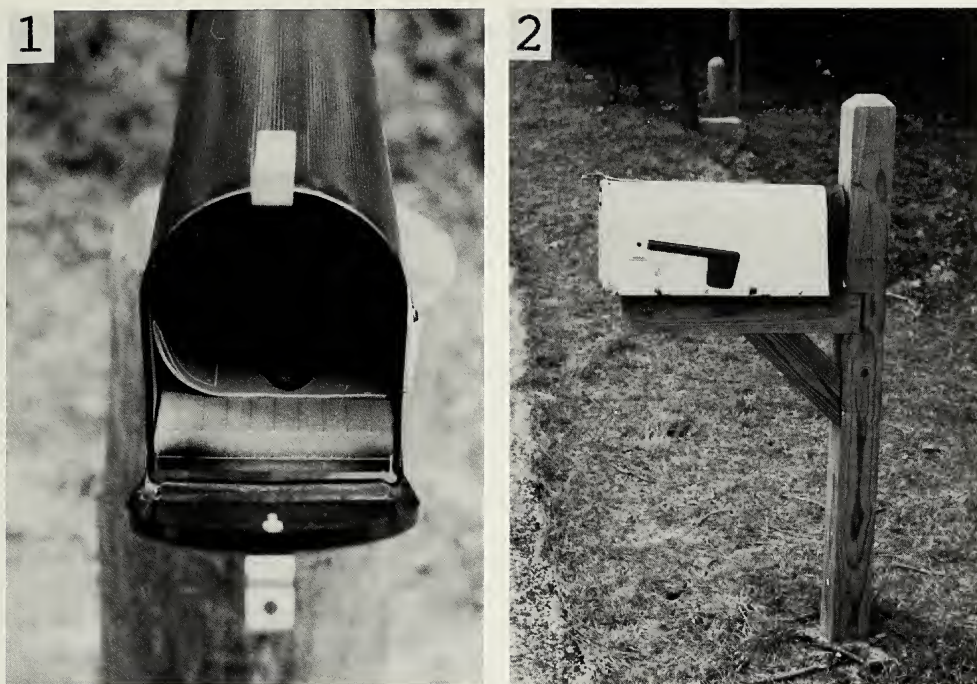
Defining the niche of any organism is a daunting task. Each species has a complex set of interacting biotic and abiotic requirements within which it survives (Hutchinson 1957). In the case of spiders it is difficult to define their individual niche requirements based only on the specific habitat within which they have been collected. A surprising number of species collected in well defined habitats are clearly not typical occupants of the habitat and may be considered rare or accidental. When the sampling procedure is based on a set of quadrats, a species that occurs in only one quadrat, whatever the number of individuals, is referred to as a 'unique' species (*cf.* Heltsche & Forrester 1984). The term 'unique' is neutral in that it does not presume that the species is necessarily rare or accidental within the habitat. Unique species make up a large percentage of the spider species collected in many habitats, varying from 25-50% of the total number of species collected (Edwards 1993). Spiders are vagile and accordingly tend to confuse the issue when one is attempting to describe a typical species assemblage for any particular habitat. Some insight may be

gained into the nature of unique species, the niche-spatial requirements of spider species and by the species assemblages observed from an examination of the data obtained collecting spiders from an artificial habitat; in this case the rural delivery mailboxes in Mashpee, Barnstable County, Massachusetts.

### METHODS

Typical mailboxes and their settings are shown in Figs. 1, 2. The standard box is made of galvanized sheet metal, usually 16.5 cm wide, 21.5 cm high and 48 cm long and has a rounded top (Fig. 1). The mailbox is often painted black or variously decorated by the owner. The box is supported by a pipe or stout post, *circa* 8 cm in cross section upon which it is directly seated or from which it is cantilevered and may have additional oblique supports at the bottom (Fig. 2). On sunny days these boxes may get very warm. Attendance to 350-400 such boxes, involving some 40 km of travel daily, Monday-Saturday, comprises the average route. The mailman, Eric Edwards, is familiar with the local species and collects those spiders not previously collected, or that had not been collected in any particular month. Time constraints and other factors make it impossible to observe or collect spiders from these boxes systematically. The mailbox is described and the results of the initial three years of data collection are provided in Edwards & Edwards (1991). As of July 1995, eight years of collecting and observation have been completed and 199 species (1252 individuals) of spiders collected. The





Figures 1, 2.—Photographs of rural delivery mailboxes. 1, Box fastened to top of post, front end with door open. The projecting handle at top of door and handle lock on top of box. Note space between bottom of door and box; 2, Cantilevered mailbox. Notice that post projects above the mailbox and the oblique support beneath.

mailboxes are usually situated a short distance away from vegetation other than short grass or lawn. Occasionally there will be a simple, doorless box on a slender metal stake nearby for newspaper deliveries. These boxes were not sampled. The area has many ponds and bogs, some fields, and abundant lawns, with pitch pine (*Pinus rigida* Mich.), white pine (*Pinus strobus* L.), red cedar (*Juniperus virginianus* L.) and several species of oaks (red -*Quercus rubra* L.; scarlet -*Q. coccinea* Muenshh.; and white -*Q. alba* L.) dominating the patches of woods in the surrounding areas. A large variety of shrubs, both local species and horticultural varieties, are found nearby. The mailboxes offer a unique set of spatial options to the spiders that happen upon them. These options include the outer, smooth surface, approximately 3,670 cm<sup>2</sup>, the dark interior of the box, the handle and door lock that extend up and out from the box when the door is closed, the outer bottom surface, and any space between the overlapping flange of the door and the box itself on the sides and top. The space between the bottom of the door and the box is fairly wide ( $\pm 5$  mm), and is used

as passages by many species (Fig. 1). Other than spiders, prey in the form of ants and flies are frequently found on the box. Representative collections of species have been deposited in the United States National Museum.

As in the case of agroecosystems (Rypstra & Carter 1995), the mailboxes are newly colonized each year with a large number of species that have overwintered elsewhere. The niche-spatial options offered by the mailbox represent a consistent set of microhabitats within an artificial habitat that, in turn, exists within a complex array of natural habitats.

## RESULTS AND DISCUSSION

**Unique species.**—Considering each month as a separate quadrat for the purposes of this study, 72 species (36%) of spiders collected from the mailboxes during the period June 1987–July 1995 classify as unique species (Table 1). Sixty-five of these were represented by single individuals, seven by two individuals. The two seasonal modes in the number of species, early summer and fall, are typical of the overall area. The unique species are roughly proportional to the total number of

Table 1.—Number of species collected in one month only during the period June 1987–July 1995. Collected from Mashpee, Massachusetts rural delivery mailboxes.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1987						4		2	1	1			8
1988						2				1			3
1989				2	3	6	5	1	3	2	3		25
1990	1				1	2		1					5
1991					2	1	3	1	2	1			10
1992			1			1	4					1	7
1993			1	3	1								5
1994			1			3	1		1	1			7
1995					1	1							2
Total	1	0	3	5	8	20	13	5	7	6	3	1	72

species found each month (Fig. 3), suggesting that ballooning accounts for many of these occurrences (Bishop & Riechert 1990). Over a long period of time one would expect the number of these species to diminish slowly as, by virtue of their vagility, individuals of all the species of the regional pool will eventually happen upon the mailbox. The regional pool of spiders in the Mashpee area is estimated to be approximately 500 species (Edwards 1993).

**Residential species.**—At least 39 species are found on the mailboxes much of the year and are referred to here as 'residential' species (Table 2). The boxes are disturbed to some degree on most mail days because of the large amounts of material gratuitously sent to 'Box Holder' or 'Resident Box RR04.' From time to time, large numbers of boxes are vandalized. In spite of this, many species establish more or less permanent positions with capture

webs and/or retreats in or on the box (Edwards & Edwards 1991). For example, *Steatoda borealis* (Hentz 1850) is consistently found deep inside the box where it builds its web and deposits its egg sacs. In a natural setting this spider is found in recesses in the trunks of trees and logs, but can be common also under domestic refuse, such as piles of old lumber around houses. Similarly, *Pityohyphantes costatus* (Hentz 1850) maintains a sheet web near the front end at the top of the box where it is also less affected by the act of delivering or removing mail. Other species, for example *Philodromus vulgaris* (Hentz 1847), build retreats (within which egg sacs are deposited) along the inside edges of the door and box and search for prey outside. These species move in and out of the box freely through the space at the bottom and around any other open edges of the door. Three theridiid species, *Thymoites unimaculatus* (Emerton 1882), *Theridion murarium* Emerton 1882, and *Theridion lyricum* Walckenaer 1841, and the tetragnathid *Tetragnatha viridis* Walckenaer 1841, are consistently found on the upward and outward projecting handle and door lock of the box (Fig. 1). The theridiids maintain webbing here, apparently replacing it readily despite disturbance. *T. viridis* makes no obvious organized web and seems to behave more like a mimetid spider: its presence appears to discourage the close presence of other species. We have found *T. viridis* on pines and cedars both day and night, and in all cases also without obvious capture webs (orbs). *Uloborus glomosus* (Walckenaer 1841) was observed only on white boxes, and was one of only a very few species that construct-

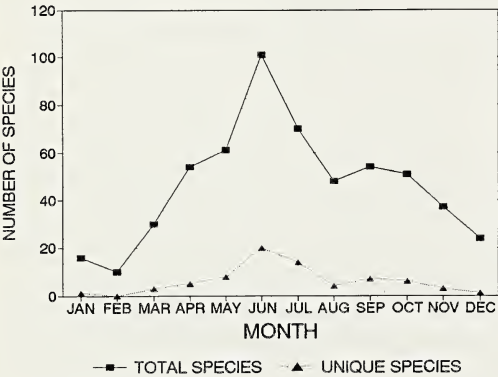


Figure 3.—The total number of species and number of unique species collected from Mashpee mailboxes, by month from June 1987–July 1995.



Table 2.—Mailbox species considered as residential. Based on collections and observations, June 1987–July 1995, Mashpee, Massachusetts. Arranged on basis of life cycle stages represented. Juv. = juvenile, Ad. = adult. The natural habitat in the Mashpee area for these species is indicated.

Species	Months	Stage	Habitat
<i>Anyphaena celer</i> (Hentz)	Mar–Oct	Juv. & Ad.	conifer
<i>Hibana gracilis</i> (Hentz)	Apr–Nov	Juv. & Ad.	conifer
<i>Araneus bivittatus</i> (Walckenaer)	Jan–Dec	Juv. & Ad.	conifer
<i>Araneus gadus</i> Levi	Mar–Dec	Juv. & Ad.	conifer
<i>Araniella displicata</i> (Hentz)	Apr–Dec	Juv. & Ad.	conifer
<i>Eustala anastera</i> (Walckenaer)	Jan–Dec	Juv. & Ad.	conifer
<i>Grammonota pictilis</i> (O.P.—Cambridge)	Mar–Nov	Juv. & Ad.	conifer
<i>Pityohyphantes costatus</i> (Hentz)	Jan–Dec	Juv. & Ad.	conifer
<i>Mimetes notius</i> Chamberlin	Feb–Nov	Juv. & Ad.	conifer
<i>Oxyopes scalaris</i> Hentz	Jan–Dec	Juv. & Ad.	conifer
<i>Philodromus rufus</i> Walckenaer	Mar–Dec	Juv. & Ad.	conifer
<i>Metaphidippus exiguus</i> (Banks)	May–Oct	Juv. & Ad.	conifer
<i>Xysticus punctatus</i> Keyserling	Mar–Dec	Juv. & Ad.	conifer
<i>Theridion lyricum</i> Walckenaer	Jan–Dec	Juv. & Ad.	conifer
<i>Theridion murarium</i> Emerton	Jan–Dec	Juv. & Ad.	conifer
<i>Thymoites unimaculatus</i> (Emerton)	May–Nov	Juv. & Ad.	conifer
<i>Clubionoides excepta</i> (C.L. Koch)	May–Sep	Juv. & Ad.	trunk
<i>Philodromus vulgaris</i> (Hentz)	Feb–Dec	Juv. & Ad.	trunk
<i>Maevia vittata</i> (Hentz)	Apr–Oct	Juv. & Ad.	trunk
<i>Rhidippus audax</i> (Hentz)	Mar–Nov	Juv. & Ad.	trunk
<i>Platycryptus undata</i> (DeGeer)	May–Sep	Juv. & Ad.	trunk
<i>Coriarachne versicolor</i> Keyserling	Mar–Sep	Juv. & Ad.	trunk
<i>Steatoda borealis</i> (Hentz)	Apr–Dec	Juv. & Ad.	trunk
<i>Theridion lyricum</i> Walckenaer	Jan–Dec	Juv. & Ad.	trunk
<i>Euryopis limbata</i> (Walckenaer)	Jun–Sep	Juv. & Ad.	trunk
<i>Leucauge venusta</i> (Walckenaer)	Apr–Nov	Juv. & Ad.	understory
<i>Philodromus marxi</i> Keyserling	Apr–Sep	Juv. & Ad.	understory
<i>Tmarus angulatus</i> (Walckenaer)	Apr–Nov	Juv. & Ad.	understory
<i>Uloborus glomus</i> (Walckenaer)	May–Nov	Juv. & Ad.	understory
<i>Metaphidippus protervus</i> (Walckenaer)	Mar–Dec	Juv. & Ad.	field
<i>Misumenops asperatus</i> (Hentz)	Apr–Nov	Juv. & Ad.	field
<i>Achaearanea tepidariorum</i> (C.L. Koch)	Jan–Dec	Juv. & Ad.	house
<i>Ceratinopsis atolma</i> Emerton	Jan–Nov	Adults only	conifer
<i>Ceratinopsis nigripalpis</i> Emerton	Jan–Dec	Adults only	understory
<i>Ceratinops lata</i> (Emerton)	Apr–Sep	Adults only	trunk
<i>Eperigone maculata</i> (Banks)	Feb–Nov	Adults only	litter
<i>Philodromus laticeps</i> Keyserling	Mar–Nov	Juv. only	conifer
<i>Tetragnatha versicolor</i> Walckenaer	Jan–Dec	Juv. only	field
<i>Tetragnatha viridis</i> Walckenaer	Jan–Nov	Juv. only	conifer

ed well-defined orb webs on the box. *Phidippus audax* (Hentz 1845) is frequently encountered on the outside of the box and in retreats inside with egg sacs. One box had this species present throughout the sampling period. Although egg sacs were frequently found, most could not be positively identified to species. However, it is clear that not all the species categorized as residential fully completed their life cycle on the box. Three species present much of the year, *Philodromus laticeps*

Keyserling 1880, *Tetragnatha viridis* and *T. versicolor* Walckenaer 1841, leave the mailboxes as adults, presumably to mate and deposit egg sacs elsewhere. Both juveniles and adults of *Coriarachne versicolor* Keyserling 1880, (a darkly-colored crab spider, usually taken on pine tree trunks) and *Xysticus punctatus* Keyserling 1880, (a lightly-colored crab spider found in the foliage of conifers) are found on the boxes. These two species are found in the open in their natural habitat dur-

ing the day. Three erigonine species, *Ceratinops lata* (Emerton 1882), *Ceratinopsis atolma* Chamberlin 1925, and *Ceratinopsis nigripalpis* Emerton 1882, are present only as adults. The residential category as a whole is dominated by species most likely to be taken in coniferous foliage and on tree trunks (Table 2).

**Seasonal species.**—Thirty-five species, here categorized as 'seasonal' species, occurred consistently on the mailboxes for periods of 2–4 months, or occasionally more, during the year (Table 3). This group is dominated by species represented mostly, if not

entirely, by adults. Species normally taken in the forest understory dominate. Some are warm weather species, others cold weather species. The population of *Micrathena sagittata* (Walckenaer 1841) dramatically increased in recent years (1994–1995). Adults and a few late instars were encountered more frequently at this time, on the boxes and in webs anchored between the top edge of the box and the upper end of the supporting post (Fig. 2) or between the handle and the lower surface of the door. *Xysticus fraternus* Banks 1895, is most often found in leaf litter but shows up on boxes only as adults in June and

Table 3.—Species found seasonally on mailboxes. Arrayed by life cycle stages. Ad. = adult, Juv. = juvenile, Adults+, males+, and females+ indicates very few juveniles also found. Juv.+ indicates very few adults collected or observed. The natural habitat for these species in the Nashpee, Massachusetts area is indicated.

Species	Months	Stage	Habitat
<i>Eris militaris</i> (Hentz)	Apr–Jun	Juv. & Ad.	understory
<i>Hentzia mitrata</i> (Hentz)	May–Jun	Juv. & Ad.	understory
<i>Admetina wheeleri</i> (Peck. & Peck.)	May–Jun	Juv. & Ad.	trunk
<i>Herpyllus ecclesiasticus</i> Hentz	Jul–Oct	Juv. & Ad.	trunk
<i>Metaphidippus insignis</i> (Banks)	May–Jul	Juv. & Ad.	field
<i>Salticus scenicus</i> (L.)	Apr–Jul	Juv. & Ad.	field
<i>Tutelina similis</i> (Banks)	Jun–Sep	Juv. & Ad.	field
<i>Anyphaena pectorosa</i> L. Koch	Jun–Aug	Adults+	understory
<i>Micrathena sagittata</i> (Walckenaer)	Jun–Sep	Adults+	understory
<i>Gladicosa pulchra</i> (Keyserling)	Aug–Oct	Adults+	trunk
<i>Hyposinga rubens</i> (Hentz)	Jun–Jul	Adults+	trunk
<i>Neoscona arabesca</i> (Walckenaer)	Jul–Aug	Adults+	field
<i>Centromerus latidens</i> (Emerton)	Mar–May	Adults+	litter
<i>Ceraticelus alticeps</i> (Fox)	May–Jul	Ad. only	conifer
<i>Theridion glaucescens</i> Becker	Jun–Aug	Ad. only	conifer
<i>Agelenopsis potteri</i> (Blackwall)	Aug–Sep	Ad. only	understory
<i>Argyrodus trigonum</i> (Hentz)	Jul–Sep	Ad. only	understory
<i>Origanates rostratus</i> (Emerton)	Dec–Apr	Ad. only	understory
<i>Sciastes truncatus</i> (Emerton)	Oct–Mar	Ad. only	understory
<i>Soulgas corticarius</i> (Emerton)	Sep–Jan	Ad. only	trunk
<i>Erigone autumnalis</i> Emerton	Jan–Aug	Ad. only	field
<i>Erigone dentigera</i> (O.P.—Cambridge)	Jun–Jul	Ad. only	field
<i>Xysticus fraternus</i> Banks	Jun–Jul	Ad. only	litter
<i>Robertus pumilus</i> (Emerton)	Mar–Apr	Females+	litter
<i>Agelenopsis pennsylvanicus</i> (C.L.K.)	Aug–Oct	Females	understory
<i>Trachelus tranquillus</i> (Hentz)	Oct–Nov	Females	mailbox
<i>Dictyna minuta</i> Emerton	May–Jul	Males	conifer
<i>Frontinella pyramitela</i> (Walckenaer)	Mar–Nov	Males	conifer
<i>Zyballus bettini</i> Peckham	Jan–Sep	Males	field
<i>Meriene clathrata</i> (Sundevall)	Apr	Juv.+	litter
<i>Steatoda americana</i> (Emerton)	Apr–Sep	Juv.+	litter
<i>Dipoena nigra</i> (Emerton)	Jun–Jul	Juv.	trunk
<i>Hentzia palmarum</i> (Hentz)	Apr–Oct	Juv.	understory
<i>Pisaurina mira</i> (Walckenaer)	Aug–Oct	Juv.	understory
<i>Trabeops aurantiaca</i> (Emerton)	Mar–Jun	Juv.	litter



July. Two species of *Agelenopsis*, *pennsylvanicus* (C.L. Koch 1843) and *potteri* (Blackwall 1846), appear briefly in late summer and early fall as adult females and deposit egg sacs in the mailbox. This is consistent with their behavior in natural settings. As they mature they tend to build larger and higher funnel webs in the understory, and frequently deposit their egg sacs under loose bark or other such refugia. In one unusual circumstance, in a web shared by both a male and female *A. pennsylvanicus*, a female *Trachelus tranquillus* (Hentz 1847), had been captured. Adult females of *Trachelus tranquillus* consistently show up in the mailbox only in the fall. *Trabeops aurantiaca* (Emerton 1885) took refuge inside the box in late spring as preadult instars. At this time of the year they are taken high up on understory shrubbery, possibly as a prelude to ballooning; otherwise they tend to be found most commonly on the forest floor and in leaf litter. Several erigonine species of the genera *Erigone*, *Eperigone*, *Grammonota* and *Walckenaeria* can be abundant in lawns. Of these only adults of *Erigone autumnalis* (Emerton 1882) and *Erigone dentigera* (O.P.-Cambridge 1874) showed up regularly on the boxes. The adults of two other erigonine species, *Ceratinops lata* (Emerton 1882), and *Soulgas corticarius* (Emerton 1909) are found in the narrow space between the overlapping rim of the door and the box. They take shelter under shallow, shaded refuges on tree trunks such as those provided by lichens. Six of the seven seasonal species that included a range of instars (juveniles and adults) are salticids.

**Ballooning.**—The large number of random strands of silk observed at the uppermost part of the box, the handle, and the top of the post suggest that these positions were used as launching points for ballooning. However, no spiders were observed in the act of ballooning. This activity may account for the presence of some species, particularly those in the unique and unassigned categories.

**Distribution trends.**—There are clear trends in the numbers of species from the unique to residential categories (Table 4). Of the 199 species collected on the mailbox, 125 are represented by few records and/or sporadic occurrence and could not be assigned to either the residential or seasonal categories with any confidence (72 unique, 53 unassigned). The unique category was dominated by species

Table 4.—Habitats where species collected from mailboxes are most likely to be found in the Mashpee, Massachusetts area, for each category used in text.

	Unique	Unassigned	Seasonal	Residential
Field	36	19	7	3
Leaf litter	13	10	6	1
Understory	5	15	11	5
Conifer	5	5	4	19
Tree trunk	3	1	6	10
Around house	3	2		1
Mailbox only	7	1	1	
Totals	72	53	35	39

commonly found in fields and leaf litter. Species from such habitats decreased in number sequentially to just a few in the residential category. Species only taken on mailboxes are particularly interesting since, so far, they still remain to be taken elsewhere in this area despite intensive collecting over many years. Some examples include *Ceraticelus bryantae* Kaston 1945, reported from Connecticut; *Marpissa wallacei* Barnes 1958, which has yet to be reported further north than Georgia, and *Disembolus sacerdotalis* Crosby & Bishop 1933, apparently a rare species known only from the holotype (Millidge 1981). Few understory and coniferous species occurred as unique species with the exception of the larger species of *Araneus*. *Araneus* probably found little support in the immediate vicinity of the box for constructing orbs. *Eustala anastera* (Walckenaer 1841), on the other hand, is found year round on the box, but without webbing.

**Comments on source habitats.**—The unassigned category is dominated by species usually found in fields and on understory foliage (Table 4). Understory species dominated the seasonal category. The residential category is made up largely of species (74%) typically found on two types of natural habitats, coniferous foliage and tree trunks. Thirty-nine (53%) of the 74 species in the seasonal and residential categories are taken on coniferous foliage and tree trunks. These last two habitat types are the principal sources of the consistently observed mailbox spiders.

Table 5 lists 104 species taken in coniferous foliage (pitch pine and red cedar) and on the

Table 5.—Percent of quadrats occupied by species in foliage of pitch pine and red cedar and on trunks of pitch pine and oaks. Study carried out on Cape Cod, Massachusetts, 1989 and 1990 (Edwards 1993). Arrayed as categorized for species taken from mailboxes, and within each category in order by those taken on coniferous foliage only, on both foliage and trunks, and on trunks only.

	Foliage		Trunk	
	Pine	Cedar	Pine	Oak
No. of species	67	65	42	44
No. of quadrats	40	44	40	41
No. of unique species	23	15	19	22
Species not taken on mailbox				
<i>Cesonia bilineata</i> (Hentz)		2.3		
<i>Ceraticelus pygmaeus</i> (Emerton)	2.5			
<i>Misumenops formosipes</i> (Walckenaer)	2.5			
<i>Thanatus formicinus</i> (Olivier)	2.5			
<i>Walckenaeria brevicornis</i> (Emerton)	2.5			
<i>Philodromus pernix</i> Blackwall		4.5		
<i>Neriere radiata</i> (Walckenaer)		4.5		
<i>Phoroncidia americana</i> (Emerton)	2.5	2.3		
<i>Steatoda albomaculata</i> (DeGeer)	2.5	2.3		
<i>Grammonota maculata</i> Banks	5.0			
<i>Grammonota ornata</i> (O.P.—Cambridge)	5.0			
<i>Litopyllus temporarius</i> Chamberlin	2.5		2.5	2.4
<i>Achaearanea globosum</i> (Hentz)	10.0	34.1		2.4
<i>Sergiolus variegatus</i> (Hentz)				2.4
<i>Araneus pratensis</i> (Emerton)			2.5	
Species categorized as unique on mailbox				
<i>Araneus diadematus</i> Clerck	2.5			
<i>Dipoena buccalis</i> Keyserling	2.5			
<i>Araneus miniatus</i> (Walckenaer)	2.5	15.9	2.5	
<i>Theridion frondeum</i> Hentz	2.5	4.6	2.5	12.2
<i>Theridion crispulum</i> Simon	12.5	25.0	2.5	4.9
<i>Mangora gibberosa</i> (Hentz)				2.4
<i>Strotarchus picatorius</i> (Hentz)				31.7
<i>Drapetisca alteranda</i> Chamberlin			5.0	70.7
Species categorized as unassigned on mailbox				
<i>Ceraticelus similis</i> (Banks)		2.3		
<i>Ero leonina</i> (Hentz)		2.3		
<i>Philodromus placidus</i> Banks		2.3		
<i>Mangora placida</i> (Hentz)	2.5	2.3		
<i>Phidippus whitmani</i> (Peckham)	2.5	2.3		
<i>Gonatium crassipalpus</i> Bryant		6.8		
<i>Philodromus exilis</i> Banks	2.5	6.8		
<i>Theridion differens</i> Emerton	5.0	2.3		
<i>Hypselistes florens</i> (O.P.—Cambridge)	5.0	4.5		
<i>Cyclosa conica</i> (Pallas)	10.0			
<i>Araneus marmoreus</i> Clerck		11.4		
<i>Mangora maculata</i> (Keyserling)		11.4		
<i>Enoplognatha ovata</i> (Clerck)	5.0	6.8		
<i>Philodromus imbecillus</i> Keyserling	12.5	2.3		
<i>Eris pineus</i> (Kaston)	22.5			
<i>Araneus partitus</i> (Walckenaer)	2.5	2.3		2.4
<i>Theridion alabamense</i> Gertsch & Archer	5.0	13.6	25.0	36.6
<i>Nodocion floridanus</i> (Banks)				2.4
<i>Sylaceus pallidus</i> (Emerton)				2.4
<i>Tetragnatha laboriosa</i> Hentz				2.4



Table 5.—Continued.

	Foliage		Trunk	
	Pine	Cedar	Pine	Oak
<i>Tutelina elegans</i> (Hentz)			2.5	
<i>Mimetus puritanus</i> Chamberlin			2.5	
<i>Lepthyphantes sabulosa</i> (Keyserling)			2.5	
<i>Tutelina similus</i> (Banks)			5.0	
<i>Pulex habrocestum</i> (Hentz)			2.5	17.1
<i>Philodromus validus</i> (Gertsch)			60.0	2.4
Species categorized as seasonal on mailbox				
<i>Dictyna minuta</i> Emerton	5.0			
<i>Neoscona arabesca</i> (Walckenaer)	5.0			
<i>Theridion glaucescens</i> Becker	7.5			
<i>Eris militaris</i> (Hentz)	5.0	9.1		
<i>Pisaurina mira</i> (Walckenaer)	12.5	4.5		
<i>Zygoballus bettini</i> Peckham		2.3		2.4
<i>Centromerus latidens</i> (Emerton)		4.5	2.5	2.4
<i>Anyphaena pectorosa</i> L. Koch	5.0	13.6	2.5	2.4
<i>Argyroides trigonum</i> (Hentz)	20.0	13.6		7.3
<i>Gladicosa pulchra</i> (Keyserling)	2.5		15.0	22.0
<i>Frontinella pyramitela</i> (Walckenaer)	37.5	36.4	7.5	2.4
<i>Hypsosinga rubens</i> (Hentz)		2.3	57.5	39.0
<i>Diplocephalus nigra</i> (Emerton)	30.0	9.1	45.0	39.0
<i>Ceraticelus alticeps</i> (Fox)	82.5	59.1	45.0	9.8
<i>Agelenopsis pennsylvanicus</i> (C.L. Koch)				2.4
<i>Hentzia mitrata</i> (Hentz)				2.4
<i>Hentzia palmarum</i> (Hentz)				2.4
<i>Admetina wheeleri</i> Peckham & Peckham			15.0	12.2
<i>Herpyllus ecclesiasticus</i> Hentz			27.5	7.3
Species categorized as residential on mailbox				
<i>Ceratinopsis nigripalpis</i> Emerton		2.3		
<i>Eperigone maculata</i> (Banks)		2.3		
<i>Tetragnatha versicolor</i> Walckenaer		2.3		
<i>Maevia vittata</i> (Hentz)	2.5			
<i>Ceratinopsis atolma</i> Chamberlin	2.5	4.5		
<i>Philodromus laticeps</i> Keyserling	17.5			
<i>Araniella displicata</i> (Hentz)	2.5	15.9		
<i>Oxyopes scalaris</i> Hentz	20.0	15.9		
<i>Tetragnatha viridis</i> Walckenaer	15.0	29.5		
<i>Philodromus rufus</i> Walckenaer		56.8		
<i>Mimetus notius</i> Chamberlin	25.0	22.7		
<i>Anyphaena celer</i> (Hentz)	25.0	47.7		
<i>Xysticus punctatus</i> Keyserling	55.0	40.9		
<i>Misumenops asperatus</i> (Hentz)	2.5	4.5	2.5	
<i>Tmarus angulatus</i> (Walckenaer)	2.5	6.8	5.0	
<i>Uloborus glomosus</i> (Walckenaer)	10.0	4.5	2.5	2.4
<i>Pityohyphantes costatus</i> (Hentz)	5.0	13.6	2.5	
<i>Araneus gadus</i> Levi	12.5	11.4		2.4
<i>Soulgas corticarius</i> (Emerton)	2.5		17.5	9.8
<i>Philodromus marxi</i> Keyserling	10.0	18.2		2.4
<i>Metaphidippus protervus</i> (Walckenaer)	10.0	18.2	2.5	
<i>Euryopis limbata</i> (Walckenaer)	5.0	4.5	5.0	22.0
<i>Leucauge venusta</i> (Walckenaer)	12.5	11.4	2.5	12.2
<i>Hibana gracilis</i> (Hentz)	40.0	4.5	2.5	
<i>Philodromus vulgaris</i> (Hentz)	22.5	18.2	5.0	4.9
<i>Coriarachne versicolor</i> Keyserling	2.5	2.3	50.0	4.9

Table 5.—Continued.

	Foliage		Trunk	
	Pine	Cedar	Pine	Oak
<i>Thymoites unimaculatum</i> (Emerton)	17.5	25.0	20.0	2.4
<i>Araneus bivittatus</i> (Walckenaer)	32.5	38.6	5.0	
<i>Eustala anastera</i> (Walckenaer)	27.5	34.1	10.0	22.0
<i>Metaphidippus exiguus</i> (Banks)	50.0	50.0		2.4
<i>Theridion murarium</i> Emerton	72.5	47.7	2.5	2.4
<i>Grammonota pictilis</i> (O.P.—Cambridge)	52.5	81.8	2.5	
<i>Clubionoides excepta</i> (L. Koch)	25.0	27.3	55.0	43.9
<i>Theridion lyricum</i> Walckenaer	32.5	56.8	50.0	75.6
<i>Playcryptus undata</i> (DeGeer)			15.0	
<i>Ceratinops lata</i> (Emerton)			15.0	34.1

trunks of pitch pine and of oaks (red, scarlet and white). For each quadrat in these habitats, 1 m<sup>2</sup> was sampled by beating (coniferous foliage); brushing (oak trunks) and bark removal (pitch pine). For further information on collection methods used and a description of these habitats, see Edwards (1993).

Of the 104 species taken, 15 (14%) were not collected on the mailboxes; and, of these, 11 occurred in coniferous foliage only (Table 6). With the exception of *Achaearanea globosum* (Hentz 1850), these species were represented only in a small percentage of quadrats, suggesting that they occurred accidentally or were uncommon. Only eight (11%) of the 72 unique species found on the mailboxes occurred in either of the principal source habitats, with no other particular outside source suggested (Table 6). Categorized as a unique species on the mailbox, *Strotarchus piscatorius* (Hentz 1847) was taken only on the trunks of oaks where adult females

with egg sacs were found in shaded, moist crevices. A comparable niche option was not offered by the mailbox.

The majority of the 26 species in the unassigned category were also not abundant in any of the four natural habitats. Fifteen species were found in foliage habitats only, nine solely from trunk habitats, and just two on both types of habitats (Table 6), suggesting that some species with more restricted niches tend not to be attracted to the mailbox. Eight unassigned species (31%) were found in more than 10% of the quadrats in natural habitats (Table 5), although most were confined to either foliage or trunks with the exception of *Theridion alabamense* Gertsch & Archer 1942 (25.0% of pine trunks and 36.6% of oak trunks). Particularly interesting are two species that are taken abundantly and only on the trunks of pine and smooth barked trunks such as oak and beech. *Drapetisca alteranda* Chamberlin 1909 and *Philodromus validus* (Gertsch 1993) have been taken on mailboxes once and twice respectively. *D. alteranda* is one of the most abundant species collected from the relatively smooth barked oak trees (70.7% of quadrats). It produces a flimsy sheet web, vaguely circular in outline. The webbing tends to be supported by minor projections of the bark, otherwise it is essentially flat. The spider sits anchored in a depression, usually at the periphery of the web. As a consequence of its being anchored, when using a stiff brush as a sampling tool one often collects only the cephalothorax. It is unclear how this spider fixes itself to the bark. The mailbox did not offer a comparable setting. *Philodromus val-*

Table 6.—Distribution of mailbox species taken from trunks only, from coniferous foliage only, and from both foliage and trunks. T = trunk, F = foliage, TF = both trunk and foliage, n = total number of species.

Mailbox category	T	F	TF	n
Residential	2	13	21	36
Seasonal	5	4	10	19
Unassigned	9	15	2	26
Unique	3	2	3	8
Not on mailbox	2	11	2	15
Total	20	45	39	104



*idus* was the most common spider taken on pitch pine trunks, 60.0% of quadrats. It appears to prefer the rough-barked pitch pine where it takes refuge during the day in the many shallow leaf-like crevices of the bark. Again, the mailbox did not provide a comparable spatial niche. Here, again, it appears that specialization, e.g., trunks as opposed to foliage, tends to limit occurrence on the mailbox.

Of the 35 species in the mailbox seasonal category, 19 (68%) were taken in the four principal source habitats, ten of which were taken both in coniferous foliage and on pine and oak trunks (Table 6). It should be noted that the seasonal category (Table 5) includes many more abundant species than those included in the previous categories. However, one notable exception is the more abundant spider on coniferous foliage and pitch pine trunks, *Ceraticelus alticeps* (Fox 1891), found in 56.0–82.5% of quadrats. This small erigonine species occurs as well in the foliage of deciduous trees. It has been taken on mailboxes as adults only, not abundantly, suggesting a preference for truly arboreal situations. In contrast, juveniles and adults of a slightly larger erigonine species, *Grammonota pictilis* (O.P.-Cambridge 1875) also abundant in coniferous foliage, are to be found on the mailbox much of the year and categorized as residential. *Agelenopsis pennsylvanicus* and *A. potteri* females, as noted earlier, consistently appear inside the mailboxes in late summer, where they construct sheet webs both in and out of the box, and deposit their egg sacs. The collecting method used (brushing) on oak trunks is not an effective method for collecting these two species or any other spider that tends to hide underneath large pieces of dead bark. Aside from the spiders that built webs on the handle and the salticids, many of the erigonine species were found in retreats in spaces between the door flange and sides of the box or just inside the box where the floor meets the wall. Eight species (42%) were present in 10% or more of the quadrats of the natural habitats.

Most of the species in the residential category are represented in these natural habitats by relatively abundant spiders. Twenty-one were to be found in both foliage and trunk habitats, and 13 in coniferous foliage only, suggesting that the former group were more

eclectic in selecting a "home" or prone to moving about. Twenty-four (83%) of the 36 residential species were taken in more than 10% of the quadrats in one or more of the natural habitats.

It will be noted that 72 unique species were collected from the mailboxes (36% of total), and approximately the same percentage, 34% (23 unique species), from pitch pine foliage; and somewhat less, 23% (15 unique species), from red cedar foliage. On the other hand, 45% or 19 species were unique in the pitch pine trunk samples and 50% (22 unique species) in oak trunk samples, suggesting that a greater proportion of species were using the trunk as an avenue to other habitats. The percentage of species in 10% or more of the natural habitats (Table 5) that occurred in the mailbox categories increased sequentially; in the unassigned category, 31%; in the seasonal category, 42%; and in the residential category, 83%.

## SUMMARY

With the exception of the few species that deposited eggs and were subsequently observed as both juveniles and adults, none of the mailbox observations shed direct light on the manner in which various species arrived at the mailbox each year. Mailboxes are relatively isolated (see Fig. 2) and it is tempting to suggest that the presence of many species resulted from ballooning. Studies of spiders in agroecosystems, e.g., Bishop & Riechert 1990, Rypstra & Carter 1995 and Young & Edwards 1990, strongly suggest that ballooning plays a significant role in the annual repopulation of new habitats. Pitfall trap studies in various local habitats capture a surprising variety of species, typically dominated by older instars and adults. We suspect that the residential category (Table 2), including as it does species with relatively large numbers of early instars as well as adults later in the year, may be dominated by species that arrive initially as a consequence of ballooning, and that the membership of the seasonal category (Table 3) is dominated by adults of species that entered "on foot".

This report examined the pattern of niche-spatial and temporal variations observed in the spiders present on mailboxes, and is 'macroecological' in nature (cf. Brown 1995). It was not feasible, given stringent time limita-

tions and other factors, for the mailman to systematically collect and make observations. As a consequence, it is not possible to treat the mailbox data other than semiquantitatively. Nonetheless, these observations on a totally artificial habitat help to bring out emergent characteristics in spider niche selection and species assemblages. The number of unique and accidental species that parade through time and remain only briefly, initially suggests that colonization of the mailbox is almost a random process. However, the patterns observed are not as kaleidoscopic as it might first appear. There is a core assemblage on the mailbox represented by those species categorized as residential. This assemblage is periodically and consistently (and apparently successfully), challenged by other species at different and for shorter periods of time. This group in general is categorized as seasonal. In addition, there are yet other species, those in the unique and unassigned categories, which appear sporadically in time and in small numbers, and are judged to be engaged in attempts to balloon or that are unsuccessful in gaining a foothold. To a certain extent, the data for the source habitats (Table 5) suggests that comparable interactions may be involved.

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## SPIDERS AND THEIR PREY IN MASSACHUSETTS CRANBERRY BOGS

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**ABSTRACT.** Spiders from a total of 24 genera and eight families that possessed prey were collected using direct observation and sweep sampling during a survey of seven stands of wild (four sites) and abandoned (three sites) cranberry bogs in Massachusetts. Over all sites, 7009 spiders were inspected and 2.7% of all individuals possessed prey. At the wild bogs, Lycosidae and Araneidae were most commonly collected and at the abandoned bogs, Oxyopidae and Tetragnathidae were most common. A total of 11 orders of prey was observed and small Diptera (39.4% of total) (particularly Chironimidae), Collembola (18.6%), Homoptera (11.7%) (particularly Cicadellidae), and small Hymenoptera (9%) were the most common prey items. For all sites, three species of spider [*Pardosa saxatilis* Hentz (Lycosidae), *Oxyopes salticus* Hentz (Oxyopidae), and *Tetragnatha laboriosa* Hentz (Tetragnathidae)] represented 58% (109/188) of all specimens collected with prey. Sixty-seven percent of the prey recovered from *P. saxatilis* were Diptera or Collembola; another 20% were identified as Homoptera and Araneae. Collembola (35%) and Diptera (24%) were the dominant prey captured by *O. salticus*, and no predation on spiders by this species was observed. The majority of *T. laboriosa* with prey possessed chironomids (63%) or homopterans (17%). Dvac® samples of vegetation, taken during the study to determine levels of the total potential prey, showed that the most abundant orders were Collembola, Diptera, and Araneae and Hymenoptera and that the number and type of prey taken by spiders fluctuated with the relative abundance of potential prey.

Spiders (Arachnida, Araneae) are often the most ubiquitous and diverse insectivores in terrestrial ecosystems, exhibiting a variety of foraging strategies and prey preferences. Numerous surveys of spiders and their arthropod prey have been conducted in managed crop ecosystems, showing that spiders constitute a significant proportion of the predator guild (Young & Edwards 1990; Nyffeler et al. 1994); and in some systems, spiders are believed to contribute to the biological control of arthropod pests (Riechert & Lockley 1984; Nyffeler & Benz 1987; Wise 1993). Unfortunately, in comparison to undisturbed or natural environments, it is not surprising that it has also been shown that typical agroecosystems have considerably lower species diversity (Luczak 1975) and mean spider densities (Nyffeler et al., 1994). For example, in field crops, spider populations are adversely affected by intensive disturbances, including cultivation, mowing, harvesting and pesticide use.

The cranberry, *Vaccinium macrocarpon* Aiton, is a perennial vine that is native to wetlands in the northern regions of North America. On wild and abandoned stands of

cranberry, a great number of spiders can be found, but no investigations of their predatory role have been undertaken. In this article, we report the results of a study of spiders on wild and abandoned cranberry beds. We did not work on managed beds because we wished to determine the maximum levels of spider activity in the absence of extensive disturbances, particularly flooding and pesticide applications, which are typical on the majority of commercial bogs. The main objectives of this study were to identify the most abundant species of spiders and the prey of these spiders in stands of cranberry.

### METHODS

**Study sites.**—In 1992, surveys of spiders with prey items in their chelicerae were carried out in seven non-commercial cranberry bogs in eastern Massachusetts ranging in size from 0.2 to 1.2 ha. Bogs were classified as either “wild” or “abandoned” and were dominated by cranberry vines. The four wild bog sites were located in Sandwich (Sandy Neck), Truro (High Head), and Provincetown (Herring Cove and Mt. Ararat) in depressions be-

tween sand dunes. In addition to cranberry vines, other vegetation at these sites included Sphagnum moss, bayberry (*Myrica pennsylvanica* Mirbel), bog orchids (*Habernaria* spp.), round-leaved (*Drosera rotundifolia* L.) and thread-leaved (*Drosera filiformis* Raf.) sundews, poison ivy (*Rhus radicans* L.), various sedges, grasses and rushes, and other herbaceous and woody plants commonly found in undisturbed bog habitats in the region. The three abandoned bogs, located in Sandwich (Windmill) and Rochester (Mello 1 and Mello 2), were originally established for commercial cranberry production but were unmanaged for at least five years before this survey. Abandoned bogs had thick mats of cranberry vines and Sphagnum moss interspersed with grasses, brambles (*Rubus* spp.), poison ivy, small flowering shrubs, and saplings of the early successional tree species found in adjacent wooded habitats (including *Acer rubrum* L., *Pinus strobus* L., *Populus* spp., and *Betula* spp.).

Bogs were considered to be composed of three overlapping strata: (1) ground surface beneath the vines, (2) dense cranberry vines, and (3) taller vegetation (composed of grasses, bayberry bushes, and tree saplings). As hunting spiders generally forage on vegetation and web-builders trap prey from the air, we hypothesized that spiders within these strata would encounter and capture arthropod prey from the arthropod orders most commonly located there.

**Collection methods.**—Surveys of spiders and their prey were conducted at all wild and abandoned bogs on alternate weeks between 1 June–28 August 1992. During this period, seven surveys were made at each site. Direct observation and sweep sampling to obtain spiders with prey were conducted at the sites between 0930–1530 h, weather permitting. The first sampling method employed after arrival at a study site was direct observation. We divided each site into three parts of similar size, dependent on the total size of each site, using physical landmarks such as shrubs, trees, bog ditches, etc. Within each section, sampling was carried out by three observers who walked random paths for an hour. Bog vegetation was visually searched for spiders, which were aspirated into clear, 30 ml cups and inspected for the presence of prey in their mouthparts. If a spider possessed a prey item,

alcohol was added to the cup to kill the spider; and both spider and prey were brought back to the laboratory for identification. If a spider did not possess a prey item, the inspection event was recorded on a hand-held counter and the spider was released.

Next, 30 sets of five random sweeps were performed using a circular, 27.5 cm diameter cloth net, with each person sampling one-third of the bog. After five sweeps, the contents of the net were emptied into a light-colored dish pan; and spiders were quickly aspirated into cups and their mouth parts checked for prey. Spiders with and without prey were treated in the same manner as those captured during direct observation. Before leaving a site, 25 randomly-selected 0.20 m<sup>2</sup> point samples of the arthropod fauna were obtained using a Dvac® (Dvac; Ventura, California) suction device (Dietrick 1961); and contents were placed in cyanide jars and transported back to the laboratory for identification. On several occasions, bogs were saturated with water, preventing use of the Dvac® and causing arthropod samples at some sites to be discontinuous.

In addition to the seven-week surveys, two extra direct observation examinations were conducted between normally-scheduled survey weeks at each of two abandoned bogs (Mello 1 and Mello 2) and two wild bogs (Herring Cove and Mt. Ararat). Direct observations were performed in exactly the same manner as previously described; however, no sweep net or Dvac samples were taken.

**Identifications.**—The first author identified all spider specimens collected with prey in the laboratory to genus, and species when possible, using Kaston (1981). Voucher specimens preserved in 70% ethanol were sent to the American Museum of Natural History for confirmation and have been deposited in the University of Massachusetts entomology collection. Prey items removed from the mouth parts of spiders were identified to order. A few prey remains that were not identifiable were discarded and the capture event removed from the data record for the site where the spider with prey was collected. Arthropods from Dvac® samples were identified to order and preserved in 70% ethanol.

**Additional field trial.**—In 1993, we compared the effectiveness of the direct observation method we employed during 1992 with



Table 1.—Percentage of spiders collected with prey in wild or abandoned cranberry bogs in 1992.

Bog sites (ha)	No. spiders inspected	No. spiders with prey	% spiders with prey
Wild			
High Head (0.5)	947	37	3.9
Herring Cove (1.2)	962	23	2.4
Mt. Ararat (0.2)	968	36	3.7
Sandy Neck (0.8)	713	22	3.1
All wild bogs	3590	118	3.3
Abandoned			
Mello 1 (1.2)	982	23	2.3
Mello 2 (1.2)	1663	28	1.7
Windmill (1.2)	774	19	2.5
All abandoned bogs	3419	70	2.1
Total—all bog sites	7009	188	2.7

the “drunkard’s walk” (Southwood 1978) for capturing spiders with prey in the cranberry system. The latter method required the establishment of a centered transect line at a site and use of a random numbers table to select discrete areas where direct observation was performed. Two people with observation experience from the 1992 survey conducted the collection comparison. Once a point was selected, the spiders present within a 0.9 m radius were individually captured and inspected during a 15 min period. A total of four individual points was selected by each observer during an hour. Three wild bogs from the 1992 study (Mt. Ararat, Herring Cove, and Sandy Neck) were selected for the comparison of the two sampling methods. Each site was surveyed weekly using both methods between

21 July–12 August. A Wilcoxon signed rank test was used to compare the number of spiders inspected and the number of spiders collected with prey (Ott 1984).

RESULTS

**Spiders collected with prey.**—During the survey, 188 spiders with prey were collected. Twenty-four of the specimens (13%) were obtained from the additional direct observations performed at the Herring Cove, Mt. Ararat, Mello 1, and Mello 2 bogs. On average, 3.3% (118/3590) of the spiders inspected at the four wild bogs and 2.1% (70/3419) of the spiders inspected at the three abandoned bogs had prey items (Table 1).

Sixty-one percent (115/188) of the spiders collected with prey were hunters and 39% (73/

Table 2.—Families of spiders collected with prey at wild and abandoned cranberry bogs in 1992.

Spider family	Abandoned bogs		Wild bogs		All bogs	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Hunters (all)	47	67.1	68	57.6	115	61.2
Lycosidae	7	10.0	59	50.0	66	35.1
Oxyopidae	34	48.5	0	0	34	18.1
Salticidae	2	2.9	5	4.2	7	3.7
Thomisidae	2	2.9	4	3.4	6	3.2
Cubionidae	2	2.9	0	0	2	1.1
Web-builders (all)	23	32.9	50	42.4	73	38.8
Araneidae	4	5.7	37	31.4	41	21.8
Tetragnathidae	15	21.4	9	7.6	24	12.8
Linyphiidae	4	5.7	4	3.4	8	4.2
Total	70	100	118	100	188	100

Table 3.—Taxa of spiders and prey items collected in cranberry bogs in 1992. Order of prey: ARN = Araneae; COL = Collembola; DIP = Diptera; HOM = Homoptera; HYM = Hymenoptera; LEP = Lepidoptera; OTH = Others (including: Orthoptera, Psocoptera, Coleoptera, Neuroptera and Acari); TOT = Totals.

Spider family	Number of predation events							
	ARN	COL	DIP	HOM	HYM	LEP	OTH	TOT
Web-building spiders								
Araneidae								
<i>Argiope</i> spp.			2	2	3		2	9
<i>Acanthepeira</i> spp.	1							1
<i>Epeira</i> spp.			1					1
<i>Mangora gibberosa</i> (Hentz)			4	2	3	1	3	13
<i>Neoscona arabesca</i> (Walckenaer)			7	1	3			11
<i>Neoscona pratensis</i> (Hentz)			2		1			3
<i>Neoscona</i> spp.			1				1	2
<i>Singa</i> spp.			1					1
All species	1	0	18	5	10	1	6	41
Linyphiidae								
<i>Ceratinops</i> spp.		1						1
<i>Frontinella</i> spp.			1		2			3
<i>Helophora</i> spp.			1					1
<i>Neriere clathrata</i> (Sundevall)			1					1
<i>Neriere variabilis</i> (Banks)			1				1	2
All species	0	1	4	0	2	0	1	8
Tetragnathidae								
<i>Tetragnatha laboriosa</i>	0	3	15	4	0	1	1	24
All web-building spiders	1	4	37	9	12	2	8	73
Hunting spiders								
Lycosidae								
<i>Arctosa</i> spp.							1	1
<i>Lycosa</i> spp.	1							1
<i>Pardosa floridana</i> (Banks)	1	2	2	1				6
<i>Pardosa milvina</i> (Hentz)			1					1
<i>Pardosa modica</i> (Blackwell)							1	1
<i>Pardosa moesta</i> (Banks)	1		3			1		5
<i>Pardosa saxatilis</i> (Hentz)	5	12	22	5	2	3	2	51
All species	8	14	28	6	2	4	4	66
Oxyopidae								
<i>Oxyopes salticus</i> (Hentz)	0	12	8	4	2	3	5	34
Salticidae								
<i>Evarcha flammata</i> (Clerck)		1						1
<i>Habronattus</i> spp.	1							1
<i>Metaphidippus</i> spp.	1							1
<i>Paraphidippus</i> spp.		3	1					4
All species	2	4	1	0	0	0	0	7
Clubionidae								
<i>Clubiona</i> spp.		1						1
<i>Catianeira</i> spp.				1				1
All species	0	1	0	1	0	0	0	2
Thomisidae								
<i>Philodromus</i> spp.				1				1
<i>Thanatus</i> spp.	2			1			1	4
<i>Xysticus</i> spp.					1			1
All species	2	0	0	2	1	0	1	6
All hunting spiders	12	31	37	13	5	7	10	115
Totals	13	35	74	22	17	9	18	188



Table 4.—Seasonal variation in taxa of prey captured by spiders at four wild and three abandoned cranberry bogs in 1992. <sup>a</sup> Percentages = the number of insects from a specific order ÷ the total number of prey items captured by spiders during a month.

Month sampled (No. sampling events)	Orders of prey captured by spiders <sup>a</sup>														Total No.
	Araneae		Collem- bola		Diptera		Homop- tera		Hymen- optera		Lepi- doptera		Other		
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
Abandoned bogs															
June (11)	1	3.5	10	34.4	9	31.0	2	6.9	1	3.5	1	3.5	5	17.2	29
July (8)	0	0	5	22.7	9	40.9	3	13.6	1	4.6	2	9.1	2	9.1	22
August (6)	1	5.3	4	21.0	6	31.6	4	21.0	3	15.8	1	5.3	0	2.0	19
Wild bogs															
June (9)	5	25.0	7	35.0	5	25.0	2	10.0	0	0.0	0	0.0	1	5.0	20
July (13)	4	6.4	8	12.9	29	46.8	5	8.1	7	11.3	4	6.4	5	8.1	62
August (10)	2	5.5	1	2.8	16	44.4	6	16.7	5	13.9	1	2.8	5	13.9	36
All Bogs															
Season totals (57)	13	6.9	35	18.6	74	39.4	22	11.7	17	9.0	9	4.8	18	9.6	188

188) were web-builders (Table 2). Of the hunting spiders, 87% (100/115) were from the families Lycosidae (wolf spiders) and Oxyopidae (lynx spiders). Spiders from the families Araneidae and Tetragnathidae (both orb weavers) made up 89% (65/73) of the web-builders with prey. Although eight families were represented in the survey, 88% (165/188) of all the predation events we witnessed involved lycosid, oxyopid, araneid, or tetragnathid spiders.

The dominant families of hunters and web builders collected with prey differed between the wild and abandoned bogs. At the wild bogs, 81% (96/118) were lycosids and araneids, while at abandoned bogs, 70% (49/70) were oxyopids and tetragnathids. Lycosids and araneids were captured with prey and observed in high numbers at all of the wild bogs. All of the oxyopids captured with prey were from the abandoned Mello 1 and 2 bogs, although the presence of oxyopids at Windmill was noted during collection outings. In addition, 13 of the 15 tetragnathids with prey from abandoned bogs were obtained at the Windmill bog.

In total, 24 genera of spiders with arthropod prey from 11 orders were collected and identified during the survey (Table 3). Three species (*Pardosa saxatilis* Hentz (Lycosidae), *Oxyopes salticus* Hentz (Oxyopidae), and *Tetragnatha laboriosa* Hentz (Tetragnathidae)) represented 58% (109/188) of all specimens

collected with prey. Sixty-seven percent (34/51) of the prey recovered from *P. saxatilis* were Diptera (22/51) or Collembola (12/51); another 20% (10/51) were identified as Homoptera (5/51) and Araneae (5/51). Collembolans (35%, 12/34) and dipterans (24%, 8/34) were the dominant prey captured by *O. salticus*, and no predation on spiders by this species was observed during the survey. The majority of *T. laboriosa* with prey possessed chironomids (63%, 15/24) or homopterans (17%, 4/24). In addition to these three species, another 27% (51/188) of the spiders with prey were identified as various species of *Pardosa*, *Mangora* (Araneidae), *Neoscona* (Araneidae), and *Argiope* (Araneidae).

Thirty-nine percent (74/188) of the arthropods recovered from the chelicerae of all spiders captured with prey were dipterans. Small flies from the family Chironomidae represented 51% (37/73) of all prey captured by web building species and 32% (37/115) captured by hunting species. Other orders frequently possessed by the web-building spiders included the Hymenoptera (16%, 12/73) and Homoptera (12%, 9/73). In addition to Diptera, the most common prey of spiders in the hunter guild were Collembola (27%, 31/115), Homoptera (11%, 13/115) and Araneae (10%, 12/115).

During the months that sampling was conducted, fluctuations in the proportions of arthropod orders possessed as prey by spiders

Table 5.—Seasonal variation in potential prey at four wild and three abandoned cranberry bogs in 1992. Potential prey orders: Percentages = the number of insects from a specific order ÷ the total number of potential prey collected during a month.

Month sampled (No. sampling events)	Araneae		Collembola		Diptera	
	No.	%	No.	%	No.	%
Abandoned bogs						
June (8)	150	3.9	1534	40.3	1417	37.3
July (5)	392	7.7	2558	50.4	558	11.0
August (4)	942	30.0	1267	40.3	456	14.5
Wild bogs						
June (7)	99	2.7	2143	59.1	664	18.3
July (11)	798	11.4	1944	27.7	1801	25.7
August (7)	550	22.3	516	20.9	600	24.4
All Bogs						
Season totals (42)	2931	11.7	9962	39.6	5496	21.9

at the wild and abandoned bogs were evident (Table 4). Between June–August at the wild and abandoned bogs, the proportion of homopteran and hymenopteran prey captured by spiders increased, while the proportion of collembolan prey taken decreased. During the same interval, the proportion of the total prey from the orders Lepidoptera and Diptera was greatest in July. Araneid prey items comprised a larger proportion of the total prey taken by spiders at the wild bogs(from 6–25%) than at the abandoned bogs (from 0–5.3%) throughout the study.

**Potential prey.**—Dvac® samples taken during June, July, and August showed fluctuations in the abundance of potential prey (arthropods available to foraging spiders). The number of arthropods collected per sample was greatest during July at both wild and abandoned bogs (Table 5).

Collembola were the most abundant potential prey at the abandoned sites, comprising 40–50% of all arthropods collected each month. In addition, the emergence of chironomids in June, adult Lepidoptera in July, and oxyopid spiderlings in August was reflected in the composition of the samples from the abandoned bogs.

At the wild sites, the proportion of Collembola steadily declined from 59% (2143/3628) of the total potential prey in June, to just 21% (516/2464) in August. During July, increased numbers of arthropods from the orders Araneae, Diptera, Homoptera, and Hymenoptera

were evident in the samples from the wild sites. Of the total potential prey present in Dvac® samples from all wild and abandoned sites throughout the survey, the most abundant orders were (in descending order) Collembola, Diptera, Araneae and Hymenoptera.

**Comparison of collection methods.**—Of the two collection methods we employed in the cranberry system, direct observation was generally more effective for capturing spiders with prey than sweep netting. Although the mean number of spiders inspected using the two methods was similar over all seven sites surveyed, the mean number of spiders collected with prey was greater using the direct observation method ( $P = 0.0001$ , Wilcoxon signed rank test) (Table 6).

During the field trial conducted in 1993, the protocol for direct observation used in the 1992 survey resulted in both a greater mean number of spiders inspected ( $P = 0.001$ , Wilcoxon signed rank test) and collected with prey ( $P = 0.003$ , Wilcoxon signed rank test) than the “drunkard’s walk” method (Table 7).

DISCUSSION

**Spiders collected with prey.**—Over all sites, approximately 2.7% (188/7009) of the spiders that we inspected possessed prey. In the literature, the percentage of hunting spiders collected while feeding ranges from 1.4–8.3% (Nyffeler et al. 1987b, 1989; Young 1989), while <10%–12% has been reported for web-builders (Nyffeler et al. 1989; LeSar



Table 5.—Extended.

Homoptera		Hymenoptera		Lepidoptera		Other		Total No.
No.	%	No.	%	No.	%	No.	%	
136	3.6	448	11.8	33	0.9	83	2.2	3801
204	4.0	565	11.1	633	12.5	170	3.3	5080
80	2.6	261	8.3	72	2.3	64	2.0	3142
228	6.3	357	9.8	21	0.6	116	3.2	3628
786	11.2	932	13.3	190	2.7	557	8.0	7008
166	6.7	295	12.0	221	9.0	116	4.7	2464
1600	6.4	2858	11.4	1170	4.6	1106	4.4	25 123

& Unzicker 1978). Although collecting technique, vegetational architecture, spider species, potential prey and several other factors varied among the studies, the average percent of spiders with prey in unmanaged cranberry systems falls within the range of that found in other systems.

Of the total spider fauna found in field crops grown in the United States, 56% are estimated to be hunting species and 44% web-building species (Young & Edwards 1990). Surveys performed in alfalfa, peanuts, rice, and cotton cite percentages ranging from 42–93 for hunting spiders and 17–58 for web-builders (Wheeler 1973; Agnew & Smith 1989; Heiss & Meisch 1985; Whitcomb et al. 1963). We found the proportions of spider types collected with prey in cranberries to be similar to these other crops, i.e., 61% were hunting species and 39% web-building species. Though the diversity of species was not determined, it is likely that these values reflect the general composition of spider types present on cranberry bogs.

The feeding trends of spiders collected with prey at wild and abandoned cranberry bogs indicate that many of the web-building and hunting species present have a varied diet that is dominated by adult dipterans. Of the 188 spiders collected with prey, 51% of all web-builders and 32% of all hunters possessed dipteran prey. Relatively high proportions of Diptera (up to 77.8% of all prey captured) have also been reported in the diets of many web-

building and hunting spiders in soybean, cotton, wheat field, alfalfa, and grassland ecosystems (Nyffeler et al. 1994). In general, spiders collected with prey in cranberries possessed arthropods of types located in the microhabitat where the spider’s foraging activity was concentrated; hunters possessed prey from the ground and the cranberry vine strata, web-builders prey from the vine and tall vegetation strata.

Prey data for hunting spiders in many systems indicate that although a variety of arthropod taxa are accepted, the groups most commonly captured include Collembola, Diptera, Heteroptera and Araneae (Edgar 1969; Hallander 1970; Yeargan 1975; Nyffeler et al. 1992, 1994). In addition to dipterans, most hunting spiders in cranberries possessed prey from orders located primarily on the ground or in the vines of bog, specifically, Collembola (27%), leafhoppers (11%), and immature spiders (10%).

The species of hunting spiders most frequently collected with prey in cranberry were *Pardosa saxatilis* Hentz and *Oxyopes salticus* Hentz. *P. saxatilis* was collected with a wide range of prey that was dominated by Diptera and Collembola, but occasionally included species of leafhoppers that vector cranberry false blossom disease and Lepidoptera whose larvae are foliar pests in the cranberry system. Yeargan (1975) observed that, despite an abundance of lepidopterans in alfalfa, the diet of the lycosid *Pardosa ramulosa* McCook

Table 6.—Comparison of the mean number of spiders inspected and collected with prey using direct observation and sweep net methods in 1992. <sup>a</sup> Spiders with prey collected during additional visits to sites were not used in comparison calculations. *n* = 21 hours for direct observations and *n* = 210 sets of five sweeps for sweepnet samples at each bog. <sup>b</sup> Significantly more spiders with prey were collected using the direct observation method (*P* = 0.0001, Wilcoxon signed rank test).

Bog	Method used <sup>a</sup>	Mean number ± SE	
		Inspected	Collected with prey
High Head	Direct observation	25.0 ± 2.7	1.6 ± 0.4
	Sweepnetting	20.0 ± 2.1	0.1 ± 0.1
Herring Cove	Direct observation	24.7 ± 1.9	0.8 ± 0.2
	Sweepnetting	19.0 ± 2.4	0
Mt. Ararat	Direct observation	24.2 ± 2.2	1.2 ± 0.3
	Sweepnetting	14.7 ± 1.4	0
Sandy Neck	Direct observation	26.2 ± 3.9	1.0 ± 0.2
	Sweepnetting	7.7 ± 1.3	0
Mello 1	Direct observation	21.7 ± 2.2	0.7 ± 0.2
	Sweepnetting	19.0 ± 3.2	0.2 ± 0.2
Mello 2	Direct observation	32.8 ± 4.0	0.6 ± 0.2
	Sweepnetting	78.7 ± 37.9	0.4 ± 0.1
Windmill	Direct observation	17.8 ± 2.3	0.7 ± 0.2
	Sweepnetting	19.3 ± 3.2	0.2 ± 0.1
All bogs	Direct observation	24.6 ± 1.1	1.0 ± 0.1 <sup>b</sup>
	Sweepnetting	25.5 ± 5.7	0.1 ± 0.0

consisted primarily of prey from the orders Homoptera, Diptera, and Araneae. Yeargan concluded that the predation exhibited by *P. ramulosa* may have been due to the rarity of encounters with Lepidoptera, which were located in the foliage above areas where the spiders most often foraged, and to attractiveness of the sudden movements often made by homopteran and dipteran prey. Although lepidoptera were scarce in the bogs we sampled,

these factors may have affected the prey selection we observed for *P. saxatilis*.

Predation of spiders by oxyopids has been reported in several surveys conducted in cotton and wooley croton, *Croton capitatus* Michaux, in Texas (Nyffeler et al. 1987a, 1987b, 1992). However, Lockley & Young (1987) noted a conspicuous lack of spiders possessed as prey by *O. salticus* in cotton in Mississippi, USA. Our data on the feeding behavior of *O.*

Table 7.—Comparison of the mean number of spiders inspected and collected with prey using the “drunkard’s walk” and 1992 direct observation methods. <sup>a</sup> *n* = 8 h for each method at each site. Significantly more spiders were inspected<sup>b</sup> (*P* = 0.001, Wilcoxon signed rank) and collected with prey<sup>c</sup> (*P* = 0.003, Wilcoxon signed rank) using the direct observation technique.

Bog	Method used <sup>a</sup>	Mean number ± SE	
		Inspected	Collected with prey
Herring Cove	Drunkard’s walk	9.5 ± 3.0	0.3 ± 0.3
	Direct observation	54.8 ± 7.3	2.8 ± 0.5
Mt. Ararat	Drunkard’s walk	22.8 ± 2.1	0.5 ± 0.3
	Direct observation	50.0 ± 5.6	3.5 ± 1.5
Sandy Neck	Drunkard’s walk	8.5 ± 3.5	0.5 ± 0.5
	Direct observation	40.5 ± 7.2	3.3 ± 2.0
All bogs	Drunkard’s walk	13.6 ± 2.5	0.4 ± 0.2
	Direct observation	48.4 ± 4.0 <sup>b</sup>	3.2 ± 0.8 <sup>c</sup>



*salticus* in abandoned cranberry bogs concurred with the latter findings for unknown reason(s), but which may have involved the availability of more easily captured prey items.

Studies of orb-weaving spiders (Araneidae and Tetragnathidae) in temperate regions have shown that most species capture Homoptera, Diptera, and small parasitic Hymenoptera in their webs (Nentwig 1987; Culin & Yeargan 1982; Provencher & Coderre 1987). In addition, large orb-weavers (*Argiope* spp.) may feed on aculeate Hymenoptera, grasshoppers, and various other "difficult" prey (Nentwig 1985; Nyffeler et al. 1987c, 1989, 1991). Our data show that orb spiders capture winged prey, predominantly Diptera, Hymenoptera and Homoptera, flying between cranberry vines and tall vegetation in bogs. Though uncommon in our study, several large-bodied Hymenoptera and Orthoptera were captured by females of the genus *Argiope* in late August as the spiders approached maturity. The majority of prey captured by species of sheet-web spiders (Linyphiidae) were from the same orders as those captured by orb-weavers.

The web-builder *Tetragnatha laboriosa* Hentz, one of the most frequently occurring spider species in field crops in the USA (Young & Edwards 1990), has been shown to commonly capture heteropteran and dipteran prey in cotton and soybean systems (LeSar & Unzicker 1978; Culin & Yeargan 1982; Nyffeler et al. 1989). In our survey of unmanaged cranberry bogs, *T. laboriosa* was the species of web-building spider most frequently observed with prey. The orders of prey possessed most often, Diptera and Homoptera, were consistent with the dominant arthropod groups reported for this species in the agricultural systems previously mentioned.

Spiders are considered by many to be generalist predators that capture the prey species that are most abundant, and thus most often encountered, in their environment (Turnbull 1960; Riechert & Lockley 1984; Wise 1993). Comparison between the proportion of prey captured by spiders and frequencies of potential prey in cranberry bogs indicates that spider predation is influenced by prey abundance (Tables 4 and 5). Although the numbers of spiders collected with prey were low, the number and type of prey possessed by spiders fluctuated with the relative abundance of po-

tential prey as captured in Dvac® samples, for most of the arthropod orders present in the system.

Foliage-feeding lepidopteran larvae and adult cranberry weevils (*Anthonomus musculus* Say) are the primary pest insects found in commercial cranberry bogs. Of the 13 spiders captured with lepidopteran prey in non-commercial bogs, five of the prey items were larvae. Two spiders were collected with coleopteran prey items during the study; however, neither was a cranberry weevil. In sum, our data indicate that few spiders in non-commercial cranberry bogs capture pest insects such as lepidopteran larvae or weevils. This suggests that spiders with similar predation behavior in commercial bogs may not have a very high impact on insect pests, particularly low density populations such as were present in the non-commercial systems.

**Comparison of collection methods.**—Over the seven-week period of this study, direct observation was more effective than sweepnetting in collecting spiders with prey. Spiders collected using sweepnets were often damaged and rarely possessed prey. Both injury to the spiders and absence of prey was most likely the result of the sweeping motion and tumbling contents of the net. Under such conditions, it is likely that spiders entering a sweepnet with prey in their mouth parts responded by releasing their prey. Prey may have also been released by spiders as the sweep samples were emptied into the dish pan and inspected.

Mean numbers of spiders inspected and collected with prey during 1993 show that the direct observation method used in 1992 was also more effective than the "drunkard's walk" method in the cranberry system, despite the successful use of the latter method in other systems (S.E. Riechert, pers. comm.). Unlike many row crops, the cranberry bogs we surveyed were covered in dense layers of vine with little exposed substrate. Hunting spiders were only visible when they were resting or actively moving on the uppermost layer of cranberry vine. Web-building spiders often positioned themselves in grasses and shrubs above the vines where they were visible to observers. Although they were easily spotted, there were not many present in any given area of bog. Given such circumstances, the probability of locating a hunting or web-building

spider may have been improved by using the direct observation method because of the increased proportion of bog area searched by experimenters.

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## ESTRUCTURA OCULAR DE *SELENOPS COCHELETI* (ARANEAE, SELENOPIDAE)

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**ABSTRACT.** *Selenops cocheleti* Simon 1880 (Selenopidae, Araneae) have their eight eyes arranged in two rows, the first formed by six eyes and the second row by only two. The first row of eyes is formed by two anterior lateral (ALE), two posterior median (PME) and two anterior median eyes (AME). Two posterior lateral eyes (PLE) point backwards and form the second row of eyes. This study used the histological staining technique of Hematoxylin-Eosin and Mallory-Azan-Heidenhain. The specimens were fixed with Bouin, using n-Butyl alcohol as an intermediary for embedding in Paraplast. Frontal, transversal and sagittal sections (6-10  $\mu\text{m}$ ) were made. The cornea and lens of all the eyes are cuticular and laminar. Behind the lens there is a layer of cone cells with projections toward the lens. The direct eyes have two cellular types at the rhabdome. They support the pigmented cells and the sensitive cells of the retina. In the indirect eyes three cellular types are found: sensitive cells of the retina, pigmented support cells and unpigmented support cells. These eyes have a tapetum (layer which reflects the light) below the pigmented layer of the ocular cup.

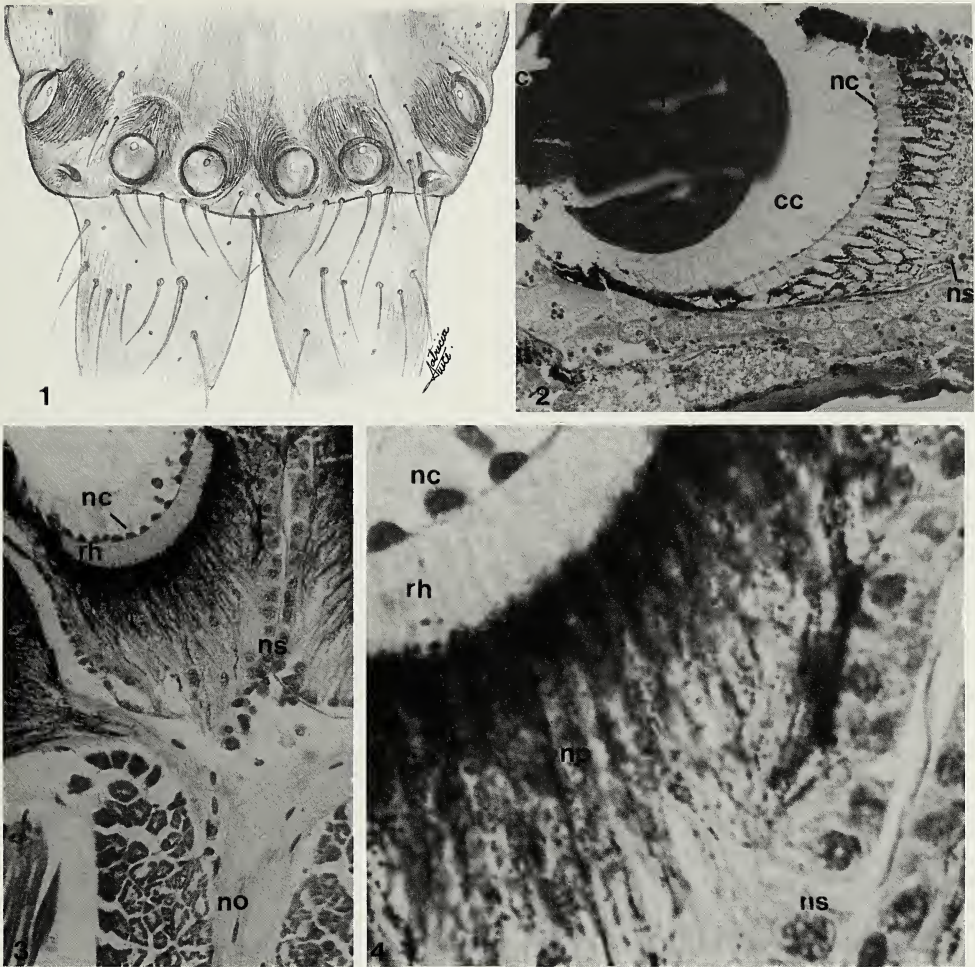
**RESUMEN.** *Selenops cocheleti* Simon 1880 (Selenopidae, Araneae) posee sus ocho ojos dispuestos en dos filas, la primera formada por seis ojos y la segunda por sólo dos. La fila anterior de ojos está constituida por dos ojos laterales anteriores (OLA), dos medios posteriores (OMP) y dos medios anteriores (OMA). Los ojos laterales posteriores (OLP) se dirigen hacia atrás y forman la segunda fila de ojos. Los OMA son ojos principales y los restantes secundarios. Para este estudio se utilizaron técnicas histomorfológicas con la coloración de Hematoxilina-Eosina y Mallory-Azan-Heidenhain. Los ejemplares fueron fijados con Bouin utilizando como intermediario alcohol n-Butílico para su inclusión en Paraplast. Se realizaron cortes a 6-10  $\mu\text{m}$ , en sección frontal, transversal y sagital. La córnea y la lente de todos los ojos son cuticular y laminar; detrás de la lente se extiende una capa uniestratificada de células cono con proyecciones hacia la lente. Los ojos principales tienen dos tipos celulares en el rhabdome; las células de soporte pigmentadas y las células sensoriales de la retina. En los ojos secundarios se reconocieron tres tipos celulares; las células de la retina, las células de soporte pigmentadas y las de soporte no pigmentadas. En éstos últimos se encuentra también un tapete (capa que refleja la luz) delante de la capa pigmentada de la copa ocular.

La disposición de los ojos de los selenópidos es característica y está relacionada con la forma achatada del cuerpo. Los ojos se disponen en una fila anterior formada por seis ojos y la posterior por sólo dos dirigidos hacia atrás, correspondientes a los ojos laterales posteriores (OLP). Los ojos medios anteriores (OMA) y medios posteriores (OMP) que en *Selenops* se disponen próximos entre sí y de manera recta o levemente recurvada en la porción central de la región cefálica (Fig. 1). Los ojos laterales anteriores (OLA), ubicados latero-externamente y separados de los ojos medios, carecen de anillo pigmentado, son per-

lados y considerados como los únicos ojos nocturnos de estas arañas (Simon 1897; F.O. Pickard-Cambridge 1900). Homann (1971) describe la estructura de los ojos de Selenopidae y la compara con los de Sparassidae. Desde ese año hasta la fecha no se ha vuelto a estudiar la estructura de los ojos de Selenopidae y se desconocen muchos aspectos relacionados a la visión y la estructura general del aparato óptico de estas arañas y las relaciones que pudieran existir con otras familias.

Este es el primer trabajo de una serie de estudio sobre la anatomía ocular de familias relacionadas con Selenopidae. En este trabajo





Figuras 1-4.—*Selenops cocheleti* Simon. 1. disposición de los ojos; 2-4. Ojo medio anterior (OMA); 2. Sección frontal (160×); 3. Sección longitudinal (250×); 4. Sección frontal mostrando rabdómeros y núcleos de las células sensoriales de la retina (1000×). Abreviaturas: OMA, ojos medios anteriores; OLA, ojos laterales anteriores; OMP, ojos medios posteriores; OLP, ojos laterales posteriores; c, córnea; l, lente; cc, células cono; nc, núcleo de célula cono; no, nervio óptico; np, núcleo de célula de soporte pigmentada; ns, núcleo de célula sensorial; rh, rabdómero.

se describe los ojos de *Selenops cocheleti* Simon.

MÉTODOS

Se utilizaron seis ejemplares, tres subadultos (1♂2♀) y tres adultos (1♂2♀), de *Selenops cocheleti* Simon capturados bajo corteza de *Eucaliptus* sp. en el Departamento Capital, Santiago del Estero, Argentina, incluidos en la colección de la Fundación Miguel Lillo (FML N° 02100 y 02101). Los especímenes voucher permanecen depositados en la histoteca de la Colección de Arácnidos de la Fundación Miguel Lillo, cuyos lotes corresponden a los números

antes mencionados. Se realizaron disecciones de las regiones cefálicas las que fueron fijadas en Bouin. El material se incluyó en Paraplast y se utilizó como intermediario en la deshidratación alcohol n-Butílico.

Se efectuaron cortes seriados de 6 y 10 µm siguiendo los planos sagital, frontal y transversal. La preparaciones fueron teñidas con Hematoxilina-Eosina y Mallory-Azan-Heidenhain.

RESULTADOS

**Ojos medios anteriores (OMA).**—*Cornea:* Cuticular, laminar con superficie externa



ondulada. Las ondulaciones se continúan en una estría transversal que la atraviesa en toda su espesor, dando un aspecto facetado (Fig. 2).

**Lente:** Se ubica por debajo de la córnea, es una estructura laminar, biconvexa, con la convexidad mayor hacia la parte interna del ojo (Fig. 2). Las láminas son más anchas que las de la córnea y acompañan la curvatura de la lente. Células cono (Eakin & Brandenburger 1971): se ubican por debajo de la lente, poseen núcleos basales ovoides, con cromatina condensada (Figs. 2, 4). Se disponen en un solo estrato con proyecciones hacia la lente. Las células cono descansan sobre una delgada membrana basal que las separa de la retina (Figs. 2-4).

**Retina:** Semilunar, formada por dos tipos celulares, las células de soporte pigmentadas y las sensoriales de la retina. Las células de soporte pigmentadas, con núcleos con cromatina granular dispuesta homogéneamente, contienen numerosos gránulos de pigmento concentrándose anteriormente formando una capa pigmentada oscura (Fig. 3). Los núcleos de estas células se disponen en diferentes planos, dando un aspecto desordenado (Fig. 4). Hacia la parte profunda, el número de gránulos de pigmento disminuye formando bandas ampliamente separadas por el citoplasma de las células sensoriales de la retina (Fig. 3).

Cada célula sensorial de la retina esta formada por la zona distal, ocupada por los rabdómeros (Figs. 3, 4), inmediatamente por debajo de la membrana basal; un segmento intermedio que atraviesa la capa oscura y clara de las células de soporte pigmentadas y la porción nuclear (Fig. 3) donde la célula aumenta su volumen. Los núcleos de las células sensoriales con cromatina granular distribuida homogéneamente (Fig. 4), se disponen periféricamente en la base de la copa ocular, emitiendo prolongaciones internas que forman el nervio óptico. En un corte transversal del ojo los núcleos de las células sensoriales se disponen en forma sublineal con las prolongaciones sensoriales a modo de paquete. Por la estructura antes mencionada estos ojos se denominan de visión directa.

**Ojos medios y laterales posteriores (OMP y OLP).**—Córnea similar a OMA. Lente biconvexa, de forma ojival y células cono semejantes a las descritas para los OMA. Retina está formada por tres tipos celulares,

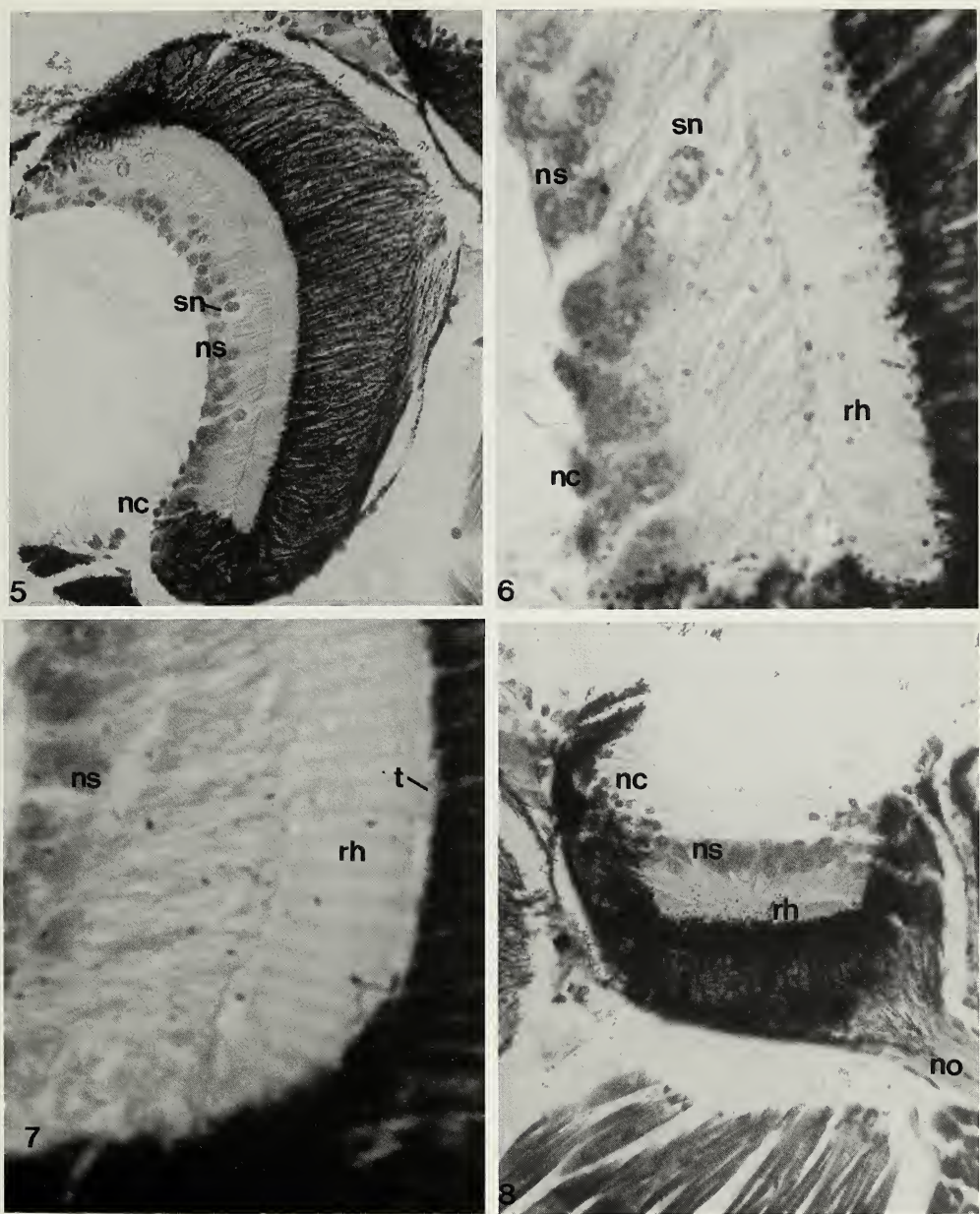
las células sensoriales de la retina (Figs. 5, 8), las células de soporte pigmentadas y las de soporte no pigmentadas (Figs. 5, 6). Existe diferencia en la estructura retiniana en los OMP y OLP. Los primeros poseen una estructura retiniana subrectangular (Fig. 8) mientras que los OLP en forma de copa (Fig. 5).

**Ojos laterales posteriores (OLP).**—Los núcleos de las células sensoriales, con cromatina distribuida homogéneamente (Fig. 6), se ubican inmediatamente por debajo de la membrana basal y otros se agrupan lateralmente entre la capa de pigmento hasta el vértice inferior. De los somas de las células sensoriales se prolongan el segmento intermedio continuándose en los rabdómeros dispuestos paralelamente (Fig. 7) cuyas prolongaciones atraviesan el reducido tapete de tipo "RT" según Homann (1971) (Fig. 7). Las células de soporte no pigmentadas son células gigantes y en número reducido (Fig. 5). El núcleo con cromatina granular, en algunos casos dispuesta periféricamente, y citoplasma claro, abundante y con proyecciones entre las fibras de las células sensoriales, a menudo acompaña a los rabdómeros llegando hasta la copa pigmentada (Figs. 5, 6). Las células de soporte pigmentadas poseen un citoplasma con mayor cantidad de gránulos de pigmento cerca de los rabdómeros y forman bandas convergentes hacia el nervio óptico, disminuyendo la concentración de gránulos de pigmento (Fig. 5). Los núcleos son difíciles de observar debido a la gran cantidad de pigmento.

**Ojos medios posteriores (OMP).**—Las células sensoriales de la retina dispuestas en por lo menos dos capas (Fig. 8), con los núcleos llegando hasta el vértice interno de la capa pigmentada (Fig. 9). Los rabdómeros se distribuyen paralelamente formando una faja subrectangular (Fig. 8). Las células de soporte no pigmentadas son grandes, con núcleos con cromatina granular, y poseen abundante citoplasma claro con prolongaciones entre las fibras de las células sensoriales de la retina, pero no atraviesan los rabdómeros (Fig. 9). Las células de soporte pigmentadas poseen mayor concentración de gránulos de pigmento en la zona de contacto con los rabdómeros y en la periferia de la copa ocular, disponiéndose entre estas regiones en bandas de menor número de gránulos de pigmento.

**Ojos laterales anteriores (OLA).**—Córnea: Cuticular, laminar, con la superficie ex-

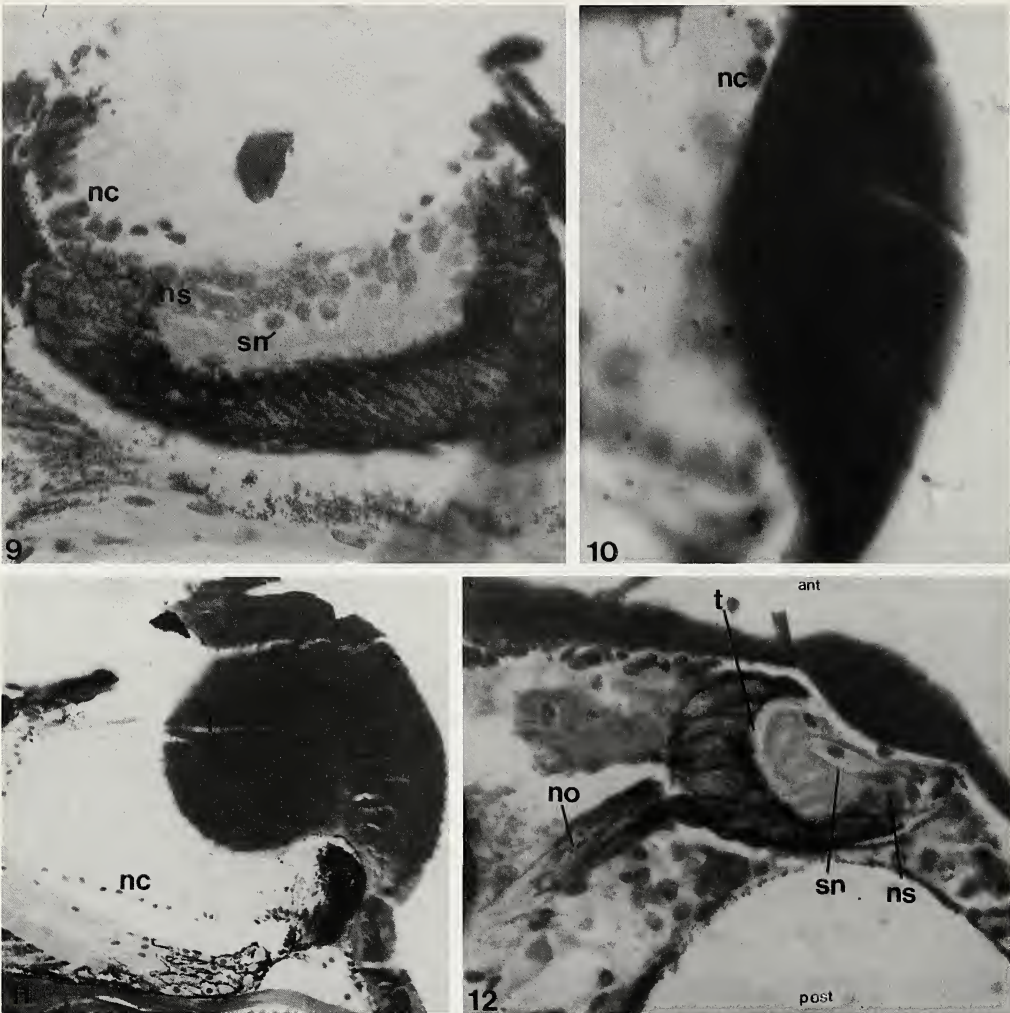




Figuras 5–8.—*Selenops cocheleti* Simon. 5–7. Ojo lateral posterior (OLP). 5. Sección longitudinal (250×); 6. Detalle de célula de soporte no pigmentada (1000×); 7. Detalle de tapete y rabdómeros (1000×). 8–9. Ojo medio posterior (OMP); 8. Sección longitudinal mostrando rabdómeros (250×); Abreviaturas: nc, núcleo de célula cono; no, nervio óptico; ns, núcleo de célula sensorial; rh, rabdómero; sn, célula de soporte no pigmentada; t, tapete.

terna con aproximadamente 4–5 placas imbricadas separadas unas de otras por estrías que atraviesan todo el espesor de la lente (Fig. 10).  
**Lente:** Laminar, ligeramente ojival (Figs. 10, 12). **Células cono:** Se ubican por debajo de la lente, sus núcleos son ovales, con cromatina muy condensada y se disponen en un

solo estrato, no observándose proyecciones hacia las lentes como en los restantes ojos (Fig. 10).  
**Retina:** Se observan tres tipos celulares, células sensoriales de la retina, células de soporte no pigmentadas y células de soporte pigmentadas. Los núcleos de las células sensoriales



Figuras 9–12.—*Selenops cocheleti* Simon. 9. Sección longitudinal mostrando células de soporte no pigmentadas (400×). 10. Ojo lateral anterior (OLA) mostrando forma de lente y superficie externa de la córnea (1000×); 11. Ojo lateral posterior, en sección frontal, mostrando forma de la córnea y lente (160×); 12. OLA, sección longitudinal mostrando disposición de núcleos de células sensoriales de la retina y células de soporte no pigmentadas (400×). Abreviaturas: ant, anterior; c, córnea; l, lente; post, posterior; nc, núcleo de célula cono; no, nervio óptico; ns, núcleo de célula sensorial; sn, célula de soporte no pigmentada; t, tapete.

se ubican en posición latero-posterior-externa del ojo (Fig. 12), emitiendo los segmentos intermedios hacia el centro de la copa ocular donde se ordenan los rabdómeros, en número escaso, dispuestos de manera semilunar y con prolongaciones que atraviesan el tapete (Fig. 12) de tipo “canoe” (KT, según Homann 1971). Las células de soporte no pigmentadas son gigantes, con cromatina granular dispuesta homogéneamente, citoplasma claro, abundante (Fig. 12) y con gruesas proyecciones hacia los somas de las células sensoriales de la

retina. Las células de soporte pigmentadas presentan los gránulos de pigmento concentrados de manera lineal detrás del tapete y periféricamente a la copa ocular, especialmente en la porción latero-posterior-externa; entre estas regiones el pigmento se distribuye desordenadamente, sin formar bandas paralelas como en los restantes ojos. El pigmento converge hacia el nervio óptico al cual acompaña en gran parte de su extensión (Fig. 12). Los núcleos de las células de soporte pigmentadas son grandes, no pudiéndose determinar la dis-



posición de la cromatina por estar enmascarada por los gránulos de pigmento.

## DISCUSIÓN

**Tipos celulares.**—En los ojos de *Selenops cocheleti* Simon se observaron diferentes tipos celulares. Los OMA (principales) presentan dos tipos celulares, células de soporte pigmentadas y células sensoriales. En los restantes ojos (secundarios) se observaron tres tipos, sensoriales, células de soporte no pigmentadas y pigmentadas.

En contraposición a los datos conocidos para Salticidae y Lycosidae (Eakin & Brandenburger 1971; Melamed & Trujillo-Cenóz 1966), las células sensoriales en la especie de *Selenops* estudiada se disponen en una sola capa en los OMA, en por lo menos dos capas en OLP y OMP y agrupadas latero-postero-externamente en los OLA. En todos los ojos (excepto OMA) se puede observar mayor concentración de núcleos de las células sensoriales en las zonas de convergencia de la luz, relacionado con la orientación de cada ojo (Figs. 5, 9, 12).

En los OMA las células de soporte pigmentadas son el único tipo de elemento de soporte, actuando como células gliales y proporcionando una matriz de sostén de las células receptoras y como una pantalla para la absorción de la luz. En los OLA, las células pigmentarias acompañan al nervio óptico en una gran extensión (Fig. 12).

Los OLA, OLP y OMP además de las células de soporte pigmentarias poseen las de soporte no pigmentadas (Figs. 5, 9, 12), las que de acuerdo con Eakin & Brandenburger (1971) actuarían, además, como células nutricias y facilitarían el intercambio de sustancias entre las células gliales y los rabdómeros. Este tipo celular fue también observado por Melamed & Trujillo-Cenóz (1966) en Lycosidae. El tamaño de estas células, en *Selenops*, con respecto al tamaño del ojo es muy destacable en los OLA (Fig. 12).

**Aparato dióptrico.**—La forma de la superficie externa de la córnea estaría relacionada con la dirección de los rayos luminosos de acuerdo con la orientación de los ojos; por lo que en los OMA, OLP y OMP la superficie externa es facetada (Fig. 11) mientras que la de los OLA es como placas imbricadas (Fig. 10). Las láminas observadas en la córnea y lente podrían, de acuerdo con Eakin & Bran-

denburger (1971), actuar como un filtro de interferencia de diferentes longitudes de onda dentro de la luz blanca. Las diferentes formas de lentes observadas podrían influir sobre la refracción de los rayos luminosos y su distribución sobre la capa receptora del ojo.

Las células cono, cuya función es la de secretar la lente (Eakin & Brandenburger 1971), en todos los ojos excepto en OLA, emiten prolongaciones anteriores que cumplirían función del “humor vítreo” de los vertebrados. En los OLA, de acuerdo con Homann (1971) las células cono se ubican inmediatamente por debajo de la lente, no existiendo proyecciones. La ausencia de “humor vítreo” en los OLA evitaría la absorción de la luz en un medio más denso, de tal manera que los rayos luminosos inciden sobre el tapete produciendo interferencia en película delgada, redistribuyendo la energía lumínica y aumentando su intensidad hacia las células receptoras ubicadas en posición latero-posterior-externa. De acuerdo con las observaciones de campo y laboratorio esta especie es de hábito crepuscular y nocturno. La función de los dos tipos distintos de tapete observados en los ojos de esta especie se desconoce.

La anatomía de los ojos secundarios ha sido utilizada para la sistemática de arañas y se sabe que las relaciones filogenéticas de Selenopidae con otras familias son confusas. Lehtinen (1967) ubica a los Cycloctenidae, Selenopidae y Zoridae en su superfamilia Lycosoidea. Homann (1968) encuentra similitud en la estructura de los ojos de *Cycloctenus* con los de *Selenops* y posteriormente (Homann 1971) los ubica en Selenopidae y sugiere que estos taxa no estarían relacionados con los Lycosoidea. Levi (1982) considera por un lado a los Lycosoidea (Stiphidiidae, Acanthoctenidae, Zoropsidae, Psechridae, Lycosidae, Pisauridae, Ctenidae, Senoculidae, Oxyopidae y Toxopidae) y por otro a los Philodromoidea (Heteropodidae, Philodromidae, Selenopidae y Cycloctenidae). Griswold (1993) estudiando los Lycosoidea (todas las familias comprendidas en Levi (1982), excepto Toxopidae) determina la monofilia del grupo sobre la base de dos sinapomorfías, una de ellas es la presencia de tapete de tipo RT, en por lo menos uno de los ojos. Selenopidae y otros taxa previamente considerados como relacionados con uno o más de los taxa tratados en ese estudio, no fueron incluidos porque de

acuerdo con Homann (1971) no están relacionados con Lycosoidea.

La presencia de tapete de tipo RT en los OLP y OMP de *Selenops* podría relacionarlos con los Lycosoidea (*sensu* Griswold 1993) y el hallazgo de un tapete KT en los OLA posiblemente los relacionaría con los Acanthoctenidae que también poseen este tipo de tapete en sus OLA.

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## A NEW SPECIES OF *CRYPsidROMUS* FROM BELIZE (ARANEAE, MYGALOMORPHAE, THERAPHOSIDAE)

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**ABSTRACT.** A new species of Theraphosidae, *Crypsidromus gutzkei*, is described (from the male only) from northern Belize. Unique coloration in combination with pedipalps of intermediate length distinguishes *C. gutzkei* from all congeners. Character states proposed as diagnostic for males of *Crypsidromus* Ausserer 1871 and *Metriopelma* Becker 1878 are combined in the male of this new species, supporting the maintenance of *Metriopelma* in the synonymy of *Crypsidromus*.

The theraphosid genus *Crypsidromus* Ausserer 1871 constitutes a taxon characterized by a dividing line of setae on tarsi IV and no tibial spurs on the mature male (Valerio 1980). *Metriopelma* Becker 1878 has often been treated as a synonym of *Crypsidromus* (Simon 1892; Petrunkevitch 1911; Roewer 1942; Gerschman & Schiapelli 1973). Twelve species once considered as *Metriopelma* are thus included with nine other species under *Crypsidromus*. However, Valerio (1982) considered *Metriopelma* a valid taxon diagnosable from *Crypsidromus* by its fused, as opposed to discrete, spermathecae. Raven (1985) argued that the contentious apomorphy of the fused spermathecae rendered *Crypsidromus* without any autapomorphic character, a situation he deemed untenable. Smith (1994) supported Valerio in restoring *Metriopelma* and suggested that the two genera could be distinguished on the basis of spination of the palpal tibia (fewer than four spines on the distal half in *Metriopelma*) and pedipalp length (longer in *Metriopelma*) in addition to spermathecal morphology. Smith cautioned that validation of *Metriopelma* based on pedipalp characteristics would depend on the collection and examination of additional specimens. The male of a new *Crypsidromus* species discovered in northern Belize exhibits a combination of *Metriopelma* and *Crypsidromus* characters which supports Raven's synonymy.

### METHODS

All measurements are in mm and were made using a dial caliper,  $\pm 0.01$  mm. Leg and

pedipalp measurements were taken from the left side. Trochanters and coxae were measured from their ventral aspect while all other leg segment measurements were taken dorsally. Description format follows Goloboff (1994). Spination abbreviations follow Prentice (1992). Standard abbreviations are used for ocular descriptions. Coloration was recorded after specimen fixation under full spectrum light using color charts in the Pantone Book of Color (Eisman & Herbert 1990).

### *Crypsidromus gutzkei* new species

Figs. 1–4, Table 1

**Type.**—Holotype male from Indian Church Village, Orange Walk District, Belize, 0.1 km W of New River Lagoon, 1 October 1995, (S.B. Reichling). Holotype deposited in the American Museum of Natural History, New York.

**Etymology.**—The specific epithet is a patronym in honor of a superb biologist and the author's scientific mentor, William H.N. Gutzke.

**Diagnosis.**—*Crypsidromus gutzkei* new species is immediately discernible from most congeners by its unpatterned abdomen, as the genus is notable among New World theraphosids for the number of species exhibiting bold abdominal patterns (Valerio 1980, 1982). The immaculate clothing of bright red setae on the abdomen of the holotype male is generically unique and distinguishes *C. gutzkei* from all Central and South American congeners with unpatterned abdomens. The male of the Mexican *C. breyeri* (Becker 1878), for

Table 1.—Leg measurements for the holotype male of *Crypsidromus gutzkei* new species. Measurements are in mm.

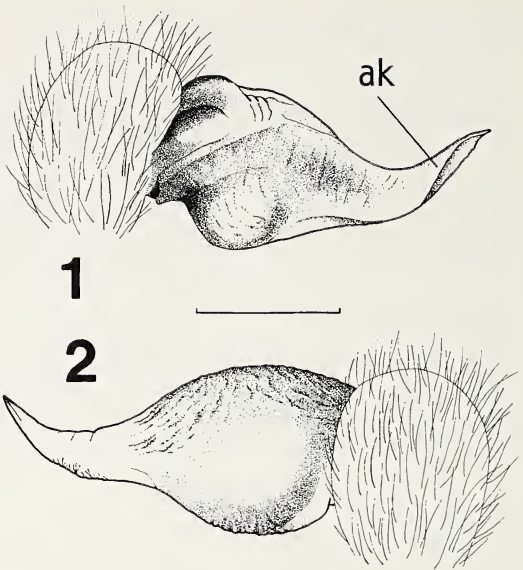
Leg	I	II	III	IV	Palp
Coxa	6.3	4.6	3.8	4.4	3.7
Trochanter	2.2	2.0	1.8	1.7	1.8
Femur	11.3	11.3	10.0	11.6	8.3
Patella	3.8	5.4	4.9	5.0	4.5
Tibia	10.8	8.8	7.8	10.2	7.2
Metatarsus	7.8	7.9	9.0	14.0	
Tarsus	5.9	5.7	5.6	6.3	1.7
Total	48.1	45.7	42.9	53.2	27.2

which the coloration in life is unknown, has longer pedipalps (exceeding tibia I in length, Smith 1994) than *C. gutzkei*.

*Crypsidromus gutzkei* is further distinguished from regional congeners by its comparatively unmodified palpal embolus. In contrast to other Central American *Crypsidromus* species, including species formerly assigned to *Metriopelma* (Valerio 1980, 1982), the apical division of the palpal embolus of *C. gutzkei* is smoothly curved, as opposed to sharply bent, and the seminal groove lacks a prominent keel. The palpal embolus of *C. gutzkei* is most similar to *C. brevibulbus* Valerio 1980 from Costa Rica. However, *C. brevibulbus* has a caput much wider than long (1.75×, Valerio 1980).

**Description.**—*Male (holotype):* Length 27.7. Carapace length 12.8, width 10.3, carapace width/length 0.80; chelicerae, width 5.0; both fang furrows with twelve macroteeth; sternum, width 4.5, length 4.4; sigilla at base of coxae I, II, and III, posterior pair largest. Labial cuspules, 130; maxillary cuspules, 208, 200. Leg span, measured from apex of left tarsus I to apex of left tarsus IV, 106.5. Pedipalps extend to just beyond the basal third of tibiae I. Leg and palp segment lengths in Table 1.

Carapace clothed in iridescent pale gold (Pantone 15–0927) pubescence, closely appressed. Dorsal surface of abdomen covered with long paprika-red (Pantone 17–1553) setae; short seal-brown (Pantone 19–1314) pubescence limited to patch of urticating hairs on posterior half of abdomen dorsum; ventral pubescence iron-gray (Pantone 18–1306). Dorsal and lateral surface of legs clothed in iridescent pale gold pubescence with scattered



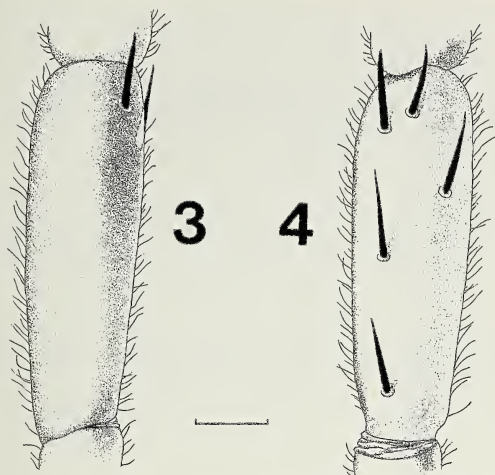
Figures 1, 2.—*Crypsidromus gutzkei* new species, male holotype. 1, Left palpal organ, retrolateral view, showing apical keel (ak) bordering seminal groove; 2, Left palpal organ, prolateral view, showing gentle curve of embolus. Scale line = 1 mm.

medium-length shale-gray (Pantone 19–3903) setae and sparsely scattered long beeswax-yellow (Pantone 14–0941) setae which grade to seal-brown basally. Ventral surface of legs lighter, with gull-gray (Pantone 17–3802) pubescence and no golden setae.

Fovea recurved. Anterior eye row slightly recurved; AME round, diameter 0.4, separated by 0.2; ALE ovoid, 0.3 × 0.4. Posterior eye row procurved; PME nearly round, diameter 0.2; PLE ovoid, 0.15 × 0.3, separated by 0.7. Caput length 1.6, width 1.2, length/width 1.33. Clypeus absent. Tibial spurs absent. All tarsi fully scopulate. Tarsi IV divided by a line of long, soft setae intermixed with dark, spiniform setae. Extent of metatarsal scopulae: I, complete; II, 0.58; III, 0.24; IV, without scopulae. Palpal bulb length 2.4, width 1.2; simple, uniformly tapering embolus; apical division without prominent bend but with gentle downward curve; keel bordering seminal groove not prominent (Fig. 1); retrolateral surface of middle division concave with several angular changes in plane, prolateral surface convex and smooth; posterior face of basal division discretely inflated (Fig. 2).

*Spination:* Leg I, metatarsus 2v(1am





Figures 3, 4.—*Crypsidromus gutzkei* new species, male holotype. 3, Left palpal tibia, dorsal view, showing two megaspines on the apical half; 4, Left palpal tibia, ventral view, showing three megaspines on the apical half. Scale line = 1.5 mm.

1m0.32), tibia 9v(2am 1ar 1ap 1p0.36 1p0.30 1p0.24 2bp); leg II, metatarsus 6v(3am 1p0.53 1r0.37 1p0.26), tibia 11v(2am 1ar 1ap 1r0.60 1m0.59 1p0.46 1m0.40 1r0.40 2bp); leg III, metatarsus 4d(1am 1ap 1m0.50 1p0.50) 12v(3am 1ar 1ap 1ep 1r0.61 1m0.46 1r0.33 2p0.33 1bp), tibia 2d(1r0.45 1br 5v(2am 1ap 2m0.50); leg IV, metatarsus 3d(1am 1r0.50 1r0.40) 14v(3am 1ar 1ap 2em 1p0.64 1r0.61 1r0.51 1m0.49 1r0.36 1m0.21 1m0.11), tibia 2d(1am 1m0.15) 4v(2am 1p0.69 1p0.29); palp, tibia 2d(1ar 1er) 5v(1am 1ap 1r0.69 1p0.49 1p0.13). Distal half of palpal tibia with five megaspines (Figs. 3, 4).

*Female*: Unknown.

**Distribution.**—Known only from the type locality. At present, *C. gutzkei* new species is the only *Crypsidromus* species reported from Belize.

**Relationships.**—The spination of the palpal tibia in combination with the intermediate length of the pedipalp apparent on the male of *C. gutzkei* suggests that spermathecal morphology may be the only diagnostic character for separation of *Crypsidromus* and *Metriopelma*. Since many *Crypsidromus* species and species formerly assigned to *Metriopelma* are known from very limited material, data describing the range of variation occurring in spermathecal and palpal bulb morphology, and spination, is unavailable. Thus, unless fur-

ther evidence is offered, *Metriopelma* should remain in the synonymy of *Crypsidromus*.

**Natural history.**—The holotype was found roaming on a sloped river bank at 2230 h, during a light rain shower. The surrounding area was secondary tropical forest extensively fragmented by small agricultural plots. In light of the intensive research on theraphosid spider ecology that has been underway in the area for over a year, the fact that only one specimen of this new taxon has been encountered suggests that *C. gutzkei* is rare.

**Material examined.**—The holotype and the following: *Crypsidromus breyeri*: MEXICO: Guanaquato (A. Duges) (BMNH).

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## THE SPIDER FAMILY CYATHOLIPIDAE IN MADAGASCAR (ARANEAE, ARANEOIDEA)

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**ABSTRACT.** The family Cyatholipidae is newly recorded from Madagascar, including the following new taxa: *Ulwembua ranomafana* new species, and *Ulwembua antsiranana* new species; *Vazaha toamasina* new genus new species; and *Alaranea* new genus, including *Alaranea betsileo*, *Alaranea alba*, *Alaranea merina*, and *Alaranea ardua*, all new species.

Madagascar is widely recognized as being of great conservation importance (National Research Council 1980; Rasoaanaivo 1990) because the island is known for high rates of endemism and unique occurrence of primitive members of otherwise widespread taxa (Myers 1988). Ongoing rapid habitat destruction, particularly of forests, makes the collection, description, and study of the evolutionary and biogeographic significance of the Malagasy biota particularly urgent. Nevertheless, the spider fauna of Madagascar remains poorly known. The number of spider species recorded from the whole island only slightly exceeds 400 (V. Roth *in lit.*), significantly less than the 626 species recorded from the British Isles (Merrett, Locket & Millidge 1985; Merrett & Millidge 1992). Yet, nearly 400 species have been collected from a single site in the southern part of the island (V. Roth pers. comm.), suggesting a rich fauna. Alderweireldt & Jocqué (1994) suggest that the known component of the Malagasy spiders fauna is around 10%, a figure rendered more credible by the recent discovery of a hitherto unknown spider family (Jocqué 1994). Given the current state of our knowledge, the discovery of Cyatholipidae in Madagascar is not surprising.

The Cyatholipidae were previously known from Africa, Jamaica, New Zealand and Australia (Griswold 1987; Forster 1988; Simon 1894). Three species from Baltic amber are attributed to this family (Wunderlich 1993). Seven new species belonging to three genera, two of them new, are herein described from Madagascar. Two new species, *Ulwembua ranomafana* and *U. antsiranana*, have their

congeners in southern Africa. A new genus, *Alaranea*, appears to be closely related to an undescribed genus from the mountains of eastern Africa. The affinities of the new genus *Vazaha* are enigmatic.

All of the new species occur in moist forests, where some may be very common. The new species *Alaranea betsileo*, *A. merina*, and *Ulwembua antsiranana* are among the most common arboreal spiders in the forests where they occur. Dozens may be found in an hour of collecting. All hang beneath sheet webs (see Davies 1978). That these common spiders were previously undescribed underscores the poor state of our current knowledge of the Madagascar spider fauna.

The material upon which this study was based was largely collected by the author and colleagues Nikolaj Scharff, Jonathan Coddington, Scott Larcher and Rija Andriamasamanana during October–December 1993. Most material collected during that period is divided among the California Academy of Sciences (CAS), Zoological Museum, University of Copenhagen (ZMUC), and Smithsonian Institution, Washington D.C. (USNM). Additional material was made available through the courtesy of J. Coddington of the USNM, R. Jocqué of the Musée Royal de L'Afrique Centrale, Tervuren (MRAC), H. Levi of the Museum of Comparative Zoology, Harvard (MCZ), C. Rollard of the Muséum National d'Histoire Naturelle, Paris (MNHN), and Vincent and Barbara Roth.

### METHODS

Prior to examination with a Hitachi S-520 scanning electron microscope all structures were

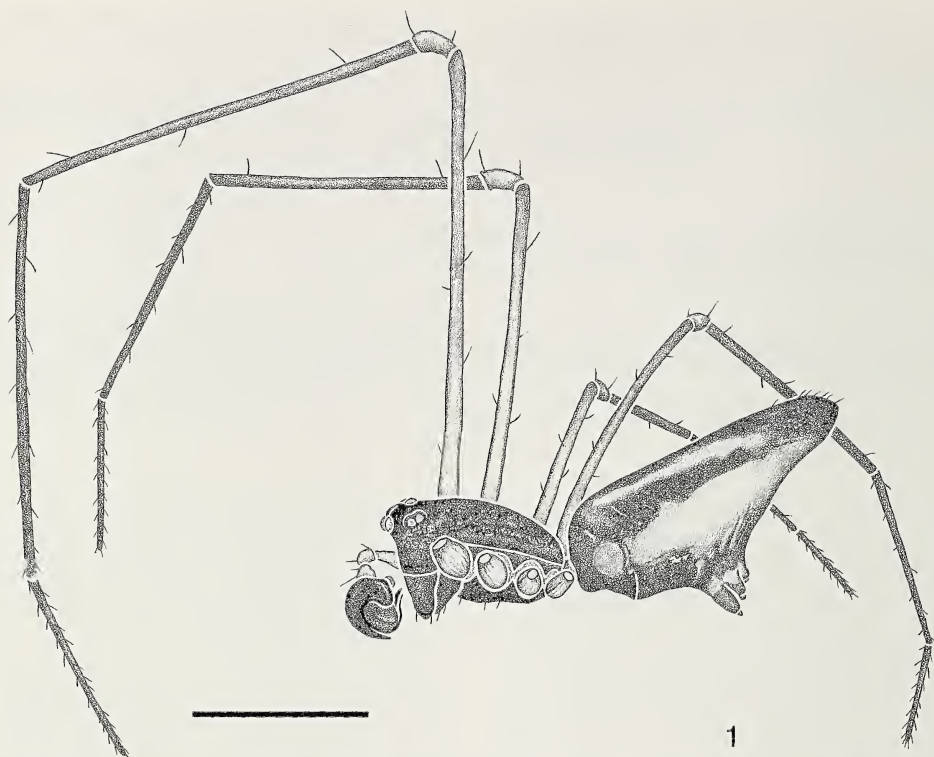


Figure 1.—*Ulwembua antsiranana* new species, holotype male, lateral view. (Scale bar = 1 mm)

critical point dried. Vulvae were cleaned by exposure to trypsin, bleached in "Chlorox" household bleach (5.25% sodium hypochlorite), stained with Chlorazol Black, and mounted in Hoyer's Medium for examination and photography. Examination was via Wild M5Apo and Leitz Ortholux II microscopes, and photography of vulvae was by an Olympus PM-10AK attached to the Leitz Ortholux II. Small structures were examined in temporary mounts as described in Coddington (1983).

Abbreviations are listed in Table 1. All measurements are in mm. Specimens measured were chosen to encompass largest and smallest individuals.

### TAXONOMY

#### Cyatholipidae Simon 1894

Cyatholipeae Simon 1894:711, based on *Cyatholipus hirsutissimus* Simon 1894. Roewer 1942:967. Cyatholipinae, Wunderlich 1978:33.

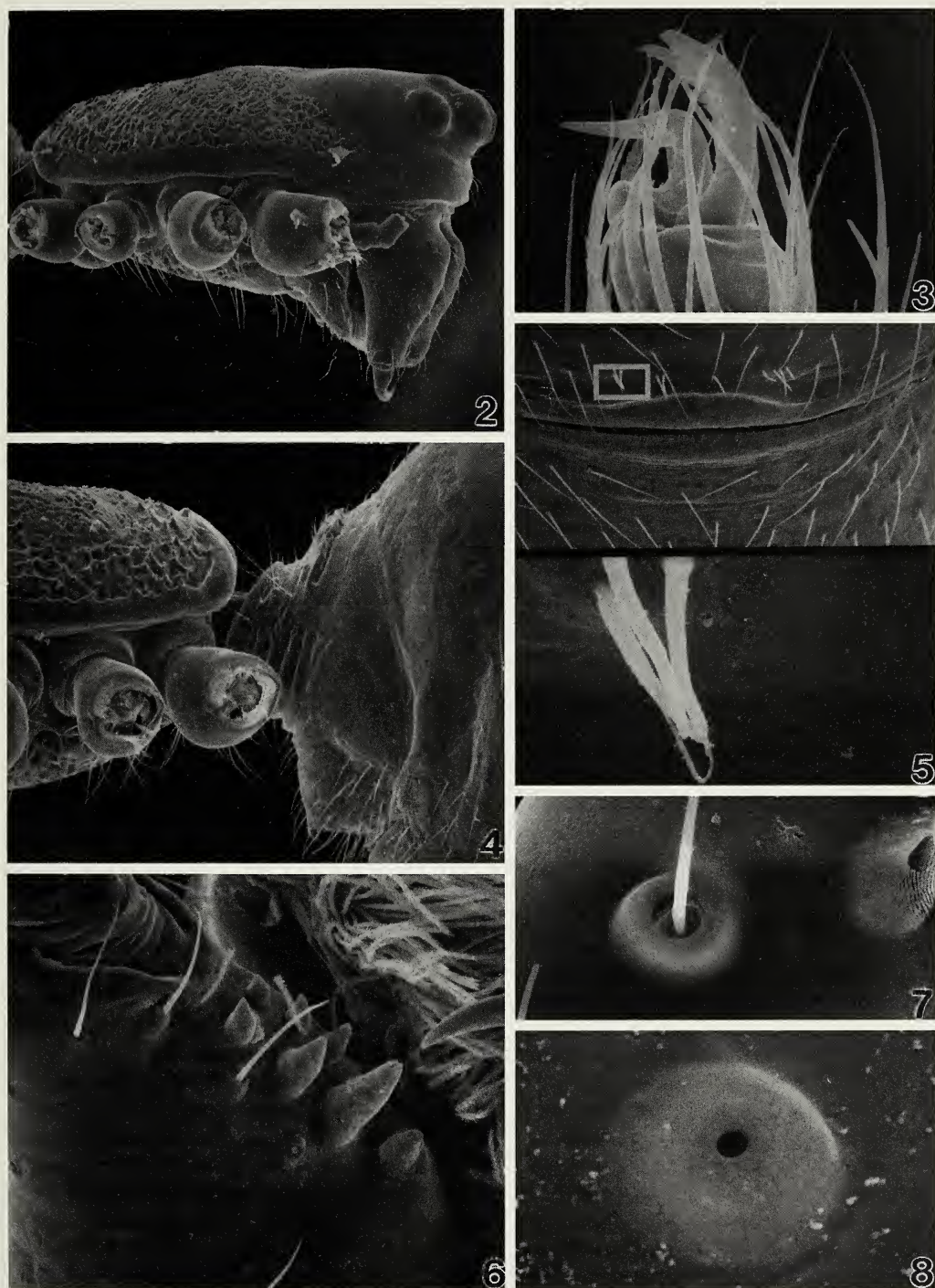
Teemenaaridae Davies 1978:42, based on *Teemenaarus silvestris* Davies 1978.

Cyatholipidae, Platnick 1979:116. Brignoli 1983:231. Griswold 1987:501. Forster 1988:7. Platnick 1989:181. Platnick 1993:172. Wunderlich 1993:234.

**Diagnosis.**—Colulate, entelegyne araneoids that share with the Synotaxidae a cup-shaped paracymbium (Fig. 33) and posteriorly broadly truncate sternum (Figs. 49, 67), and differing in having a retromedian cymbial process (Figs. 17, 33) and very broad posterior respiratory groove (Fig. 52).

**Description.**—For full description see Griswold (1987) and Forster (1988). Total length 1–4 mm; labium broader than long (Fig. 49); chelicerae smooth laterally with three small retromarginal and, in most taxa, four large promarginal teeth (Fig. 6); legs spineless (Figs. 1, 15, 68), ITC short (Fig. 3); tarsal organ (Fig. 8) and trichobothrial bases (Fig. 7) round and smooth; spinning organs (Figs. 9–14) typical of the Araneoidea in having a single ALS major ampullate gland spigot plus nubbin and 12–14 piriform gland spigots with highly reduced bases; PMS with large, anteromedian cylindrical gland spigot, two aciniform gland spigots, and posterior minor ampullate gland spigot, CY spigot absent in male; PLS with araneoid triplet of one flagelliform gland and two aggregate gland spigots, two AC spigots, and a single mesal CY spigot





Figures 2-8.—Morphology of *Alaranea* spp. 2, 4. Carapace and abdomen, lateral view; 3. Apex of tarsus I, showing claws; 5. Epiandrous region: epigastric furrow with epiandrous spigots (upper), close-up of epiandrous spigots (lower); 6. Cheliceral fang furrow, anterior; 7. Trichobothrial base, tibia I; 8. Tarsal organ, palpus; 2, 8. *Alaranea betsileo* new species, male from Talatakely; 3, 4, 6, 7. *Alaranea betsileo* new species, female from Talatakely; 5. *Alaranea merina* new species, male from Perinét.

## KEY TO THE CYATHOLIPIDAE OF MADAGASCAR

1. Abdomen not sclerotized around base of pedicel, male lacking scutum; parembolic process absent; coxae separated by soft cuticle, pleural and sternal sclerotizations separate (Figs. 1, 15, 41) ..... 2
- Abdomen sclerotized completely around base of pedicel to form annulate petiole produced dorsally into a short projection or horn (Figs. 4, 68, 94); abdomen of males with a thin, shiny transparent dorsal scutum (Fig. 95); parembolic process present (Figs. 60, 62, 73); pleural and sternal sclerotizations meet to surround coxae (Figs. 68, 94) (*Alaranea* new genus) ..... 4
- 2(1). Chelicerae with basal projection small or lacking; epigynum with median hood (Figs. 18, 19); apex of cymbial RMP directed ventrad, well separated from PC (Figs. 22, 33) (*Ulwembua*) ... 3
- Chelicerae with large basal projection (Fig. 41); epigynum lacking median hood (Figs. 29, 30, 43); apex of cymbial RMP directed distad, juxtaposed to PC (Figs. 44, 48) ..... *Vazaha toamasina* new genus, new species
- 3(2). Conductor simple (Figs. 20, 34); carapace dark except along lateral margins and on central longitudinal band extending from posterior median eyes posteriorly to behind thoracic fovea (Fig. 39); afferent duct of vulva with three loops (Fig. 36) ..... *Ulwembua ranomafana* new species
- Conductor bipartite (Figs. 16, 23); carapace light except ocular area, margins of pars cephalica, and diffuse radii from thoracic fovea on pars thoracica dark (Fig. 38); afferent duct of vulva with five loops (Fig. 35) ..... *Ulwembua antsiranana* new species
- 4(1). Males ..... 5
- Females ..... 8
- 5(4). Conductor simple (Figs. 72, 79, 88) ..... 6
- Conductor bipartite, with thin, broad proximal piece separate from conductor proper (Fig. 61) ..... *Alaranea betsileo* new species
- 6(5). Proximal point of conductor no longer than distal cup (Figs. 72, 88) ..... 7
- Proximal point of conductor elongate attenuate (Figs. 58, 79) ..... *Alaranea alba* new species
- 7(6). Proximal point of conductor small, narrower than cup (Fig. 72) ... *Alaranea merina* new species
- Proximal point of conductor thick, bifid, equal in width to cup (Fig. 88) ..... *Alaranea ardua* new species
- 8(4). Sternum dark red-brown to black (Fig. 97), abdomen of most specimens with extensive dark markings ..... 9
- Sternum pale yellow-brown, abdomen white, marked with lateral, ventral, and posterior black spots (Figs. 67-69) ..... *Alaranea alba* new species
- 9(8). Dorsum of abdomen (Figs. 65, 66, 95, 96) with longitudinal dark bands diverging from apex to middle and converging posteriorly (these bands may be bold, faint, or almost completely obscured by dark markings) ..... *Alaranea merina* and *A. ardua* new species
- Dorsum of abdomen (Figs. 63, 64) lacking such marks, most specimens with median black band surrounding 1-2 anterior white spots ..... *Alaranea betsileo* new species

(basal CY spigot universally absent in females); males retain triplet; colulus a triangular, fleshy lobe (Fig. 52); male epiandrous spigots scattered in groups of two to four anterior of epigastric furrow (Fig. 5); cymbium of male palpal tarsus with basal, cup-shaped paracymbium and retromedian process along the retrolateral margin of the cymbium just distad of the PC (Figs. 31, 33, 48, 70); palpal bulb (Figs. 31-34) with flattened, cup-shaped subtegulum and round to oval, convex tegulum; T with apical lobe, in most taxa produced ventromedially into blunt to pointed, dentate tegular lobe; T with median conductor, simple or consisting of two processes (e.g., in *Ulwembua antsiranana*, Fig. 23, and *Alaranea betsileo*, Fig. 61); embolus spirals clockwise

(left palp, ventral view), making nearly full turn, thick with truncus and pars pendula clearly distinguished; may or may not be a parembolic process at  $\frac{3}{4}$  the length of the E (Figs. 60, 62, 73); epigynum (Figs. 25-30) of most taxa with anterior, projecting scape, posterior of this a depressed atrium with transverse, median hood hiding copulatory openings that are separated by an interior median septum; cuticle laterad of epigynum probably homologous to lateral lobes of other epigyna, these may form narrow, inward-curving processes along epigastric furrow that disappear anteriorly beneath the MH; the area between these processes comprises the epigynal median lobe; vulva (Figs. 35-37) with postero-ventral copulatory openings opening into an-



Table 1.—List of anatomical abbreviations used in the text and figures.

AC	acini-form gland spigot(s)
AD	vulval afferant duct
AER	anterior eye row
AG	aggregate gland spigot(s)
AL	anterior lateral eyes
ALS	anterior lateral spinneret
A	apical lobe of tegulum
AM	anterior median eyes
AT	epigynal atrium
C	conductor
CB	cymbium
CO	copulatory opening
CY	cylindrical gland spigot(s)
E	embolus
EF	epigastric furrow
FD	fertilization duct
FL	flagelliform gland spigot(s)
HS	spermathecal head
ITC	inferior tarsal claw
LL	epigynal lateral lobes
MAP	major ampullate gland spigot(s)
mAP	minor ampullate gland spigot(s)
MH	epigynal median hood
ML	epigynal median lobe
MS	epigynal median septum
OAL	ocular area length
OQA	ocular quadrangle, anterior
OQP	ocular, quadrangle, posterior
PC	paracymbium
PER	posterior eye row
PI	piriform gland spigot(s)
PLS	posterior lateral spinneret
PL	posterior lateral eyes
PM	posterior median eyes
PMS	posterior median spinneret
PP	parembolic process
RMP	retromedian cymbial process
S	epigynal scape
ST	subtegulum
T	tegulum
TL	ventromedian tegular lobe

teriad-directed afferent duct, AD sclerotized (Figs 90–93) or hyaline (Figs. 35, 36), simple or elaborately folded, or rarely absent (Fig. 37); spermathecal head of most taxa dorsad of CO and entered laterally by AD, heavily sclerotized, nearly spherical with anterior pores; fertilization duct posterior.

*Ulwembua* Griswold 1987

*Ulwembua* Griswold 1987:532. Type species, by original designation, *Ulwembua pulchra* Griswold 1987. Platnick 1989:182.

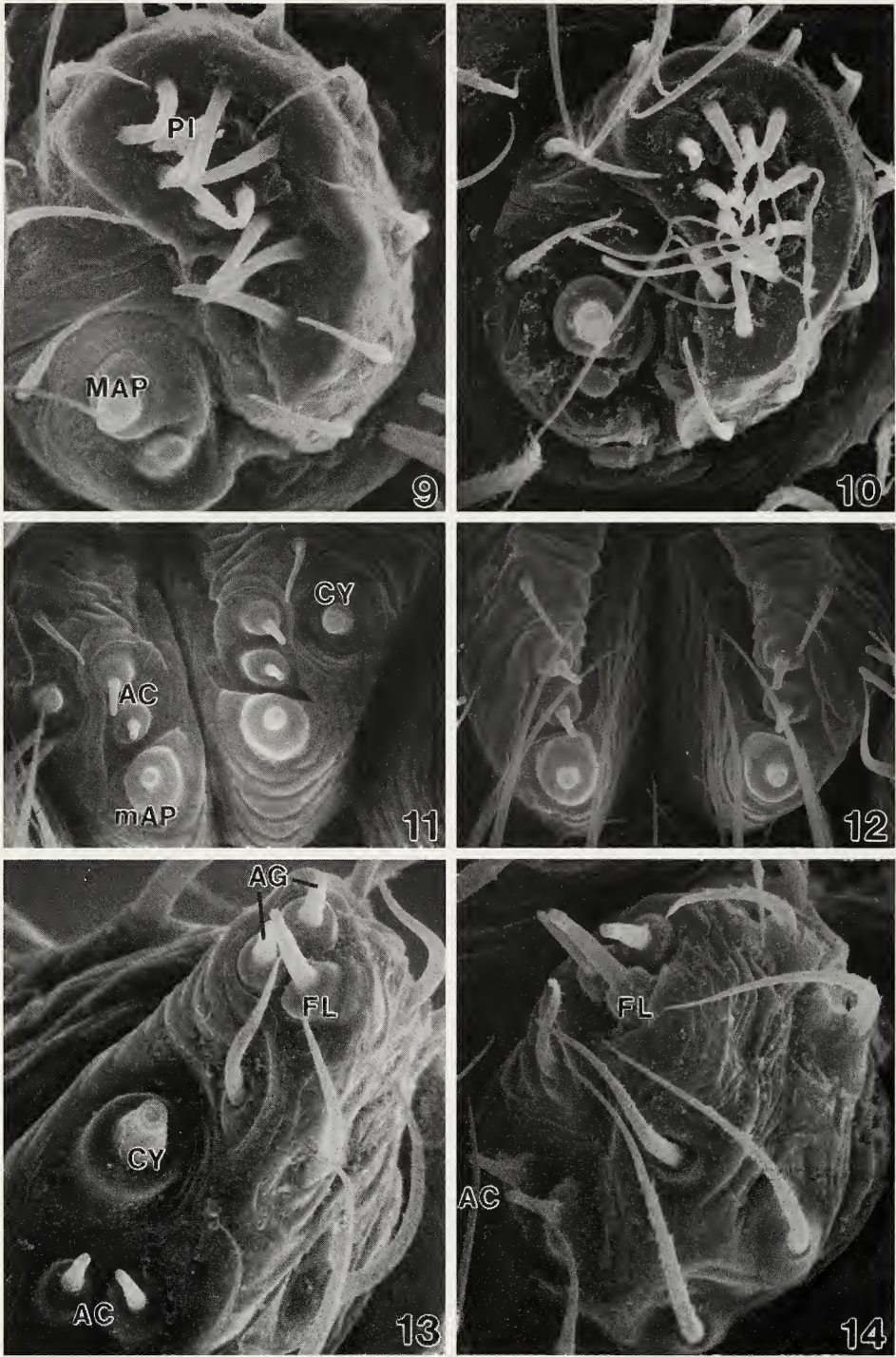
**Diagnosis.**—Abdomen triangular (Figs. 1, 15); coxae not surrounded by sclerotization; legs long, length femur I greater than 2.5× carapace width; carapace with dorsal light mark (Fig. 39); palpus lacking PP (Figs. 16, 20); vulva with extensive, hyaline AD (Figs. 35, 36).

**Description (encompasses all members of genus).**—Total length 2.00–3.32. Carapace oval in dorsal view (Figs. 38, 39), length 1.39–1.61 times width, low in most species, maximum height 0.41–0.51 width; texture finely rugose to granulate, in most specimens becoming denticulate posteriorly, thoracic fovea oval to round, indistinct, shallow in female and deeper in male; carapace posterior margin truncate to weakly concave; ocular area with PER width 1.95–2.50 times OAL, 2.30–2.80 times OQP, OQP 0.83–1.07 times OQA; diameter AM 1.00–1.80 times PM, distance PM-PL 1.07–1.85 times PM diameter; clypeal height 1.22–3.21 times AM diameter, cheliceral length 1.84–3.20 times clypeal height; chelicerae unmodified or with basal projection (*Ulwembua ranomafana*). Sternum rugose to pustulate, length 0.96–1.14 times width, coxae surrounded by unsclerotized cuticle (Figs. 1, 15). Abdomen triangular, unsclerotized or sclerotized around pedicel, not petiolate; abdominal setae short, slender, bases of anterior setae slightly enlarged. Legs long, femur I 2.5–4.5 times carapace width, unmodified. Male palpus (Figs. 16, 17, 20–24, 31–34) with cymbial RMP pointing ventrad, smaller than PC; palpal bulb with dentate TL, apex a small, smooth to pustulate lobe; C smooth, variable, median or basal, longitudinal or transverse, simple or with accessory process; E thick, long, in most species embolus makes more than 1.1 rotation, base smooth, simple, origin apical near 12 o'clock; PP absent; spermduct with tight double twist (curlicue) near embolic base. Epigynum (Figs. 18, 19, 25–28) with S and MH, septum between copulatory openings slender to broad, atrial furrows may or may not extend behind S; ML parallel-sided. Vulva (Figs. 35, 36) with extensive hyaline AD, extending anterior then posteriad to join HS; FD posterior.

**Composition.**—Five species, two in Madagascar.

**Distribution.**—Southern Africa; Madagascar (Fig. 98).





Figures 9–14—Spinnerets of *Alaranea betsileo* new species, from Talatakely. 9, 10. ALS; 11, 12. PMS; 13, 14. PLS; 9, 11, 13. Female; 10, 12, 14. Male. AC = aciniform gland spigots; AG = aggregate gland spigots; CY = cylindrical gland spigots; FL = flagelliform gland spigot; MAP = major ampullate gland spigot; mAP = minor ampullate gland spigot; PI = piriform gland spigots.



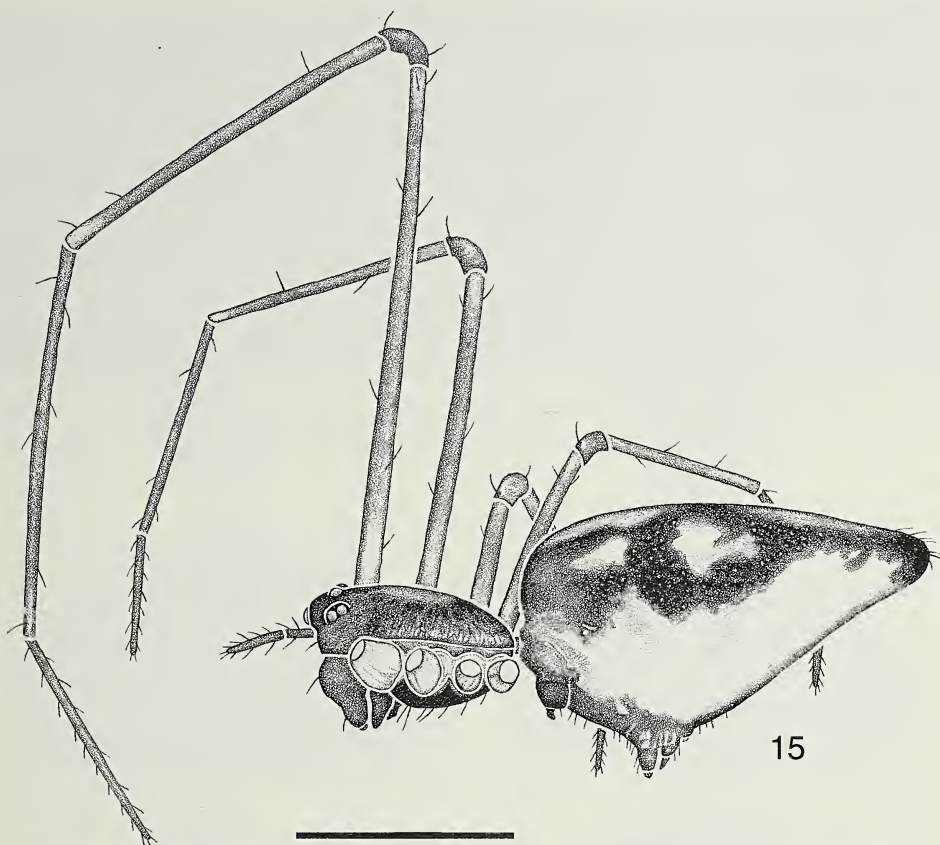


Figure 15.—*Ulwembua ranomafana* new species, paratype female, lateral view. (Scale bar = 1 mm)

*Ulwembua antsiranana* new species

Figs. 1, 16–18, 22–26, 35, 38, 98

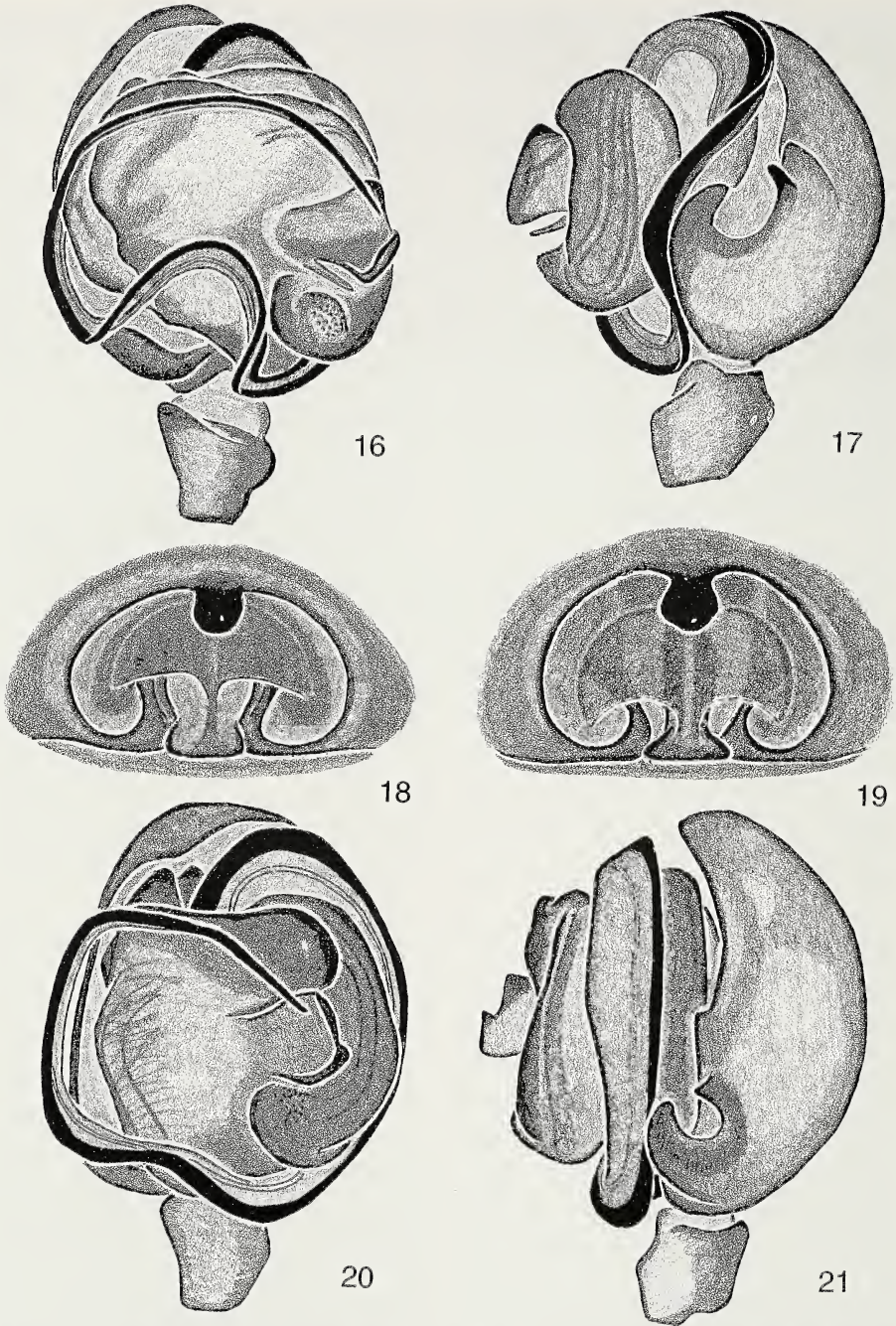
**Types.**—Male holotype and female paratype from forest at an elevation of approximately 1000 m at Parc National Montagne d'Ambre (12°32'S, 49°10'E), Antsiranana Province, Madagascar, 30 November 1993, C.E. Griswold (CAS).

**Etymology.**—Antsiranana, the province of the type locality, a noun in apposition to the generic name.

**Diagnosis.**—Carapace light except dark on ocular area, margins of pars cephalica, and diffuse radii from thoracic fovea on pars thoracica (Fig. 38). Male with E strongly sinuate across tegulum base, C double (Figs. 16, 23). Vulva with AD complex, having five loops (Fig. 35).

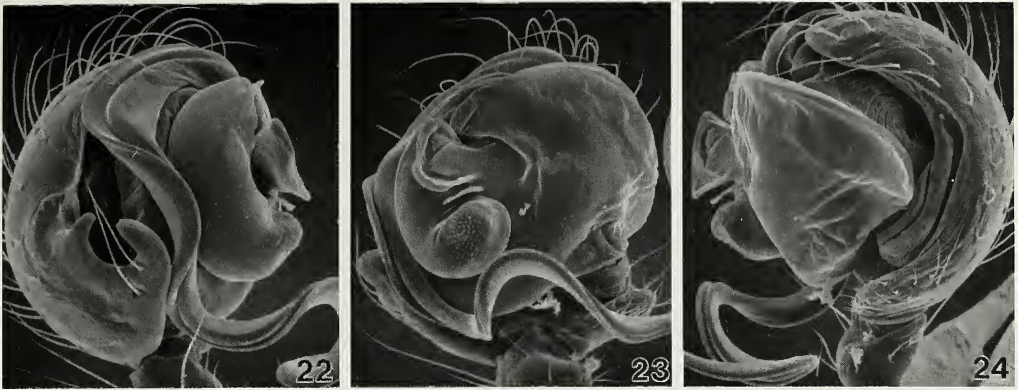
**Description.**—*Male (holotype):* As in Fig. 1. Total length 2.66. Carapace dusky yellow-gray along lateral margin, gray narrowing behind ocular area, and along margins of pars

cephalica, faintly mottled in center, with dark gray forming narrow longitudinal band anterior of thoracic fovea and faint bands radiating from thoracic fovea to margin, dorsum between these marks yellow-brown; ocular area with black surrounding and extending between AM and posterior to surround each PM, and surrounding and extending between lateral eyes; clypeus yellow-brown, dark in center from AM to oral margin; chelicerae and palpal coxae brown, labium and sternum nearly black, unmarked; coxae, trochanters, legs, and palpi yellow-white, cymbium dark brown, legs shading to yellow-gray from distally on femora to tarsi, unmarked; abdomen white, dorsum with pair of median and lateral dark gray longitudinal bands that meet at abdominal apex, venter gray from abdominal apex to pedicel. Carapace 1.08 long, 0.67 wide, 0.35 high, texture finely granulate, posterior margin weakly concave; thoracic fovea round, very shallow, with small posterior pit; PER and



Figures 16–21.—Genitalia of *Ulwembua* spp. 16, 17, 20, 21. Left male palpus; 18, 19. Epigynum; 16, 18–20. Ventral view; 17, 21. Retrolateral view; 16, 17. *Ulwembua antsiranana* new species, holotype; 18. *U. antsiranana* new species, Montagne d'Ambre; 19. *U. ranomafana* new species, paratype; 20, 21. *U. ranomafana* new species, holotype.





Figures 22–24.—Right male palpus of *Ulwembua antsiranana* new species, Montagne d'Ambre. 22. Retrolateral view; 23. Ventral view; 24. Prolateral view.

AER 0.42 wide, OAL 0.20; ratio AM:AL:PM:PL, 1.33:1.08:1.0:1.17, PM diameter 0.06. Clypeus 0.18 high, chelicerae 0.35 long, unmarked. Sternum 0.58 long, 0.56 wide, rugose; labium 0.11 long, 0.19 wide; palpal coxae 0.20 long, 0.13 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $2.85 + 0.30 + 2.62 + 2.42 + 1.19 = [9.38]$ ; II:  $2.13 + 0.25 + 1.76 + 1.55 + 0.87 = [6.56]$ ; III:  $1.13 + 0.23 + 0.85 + 0.83 + 0.53 = [3.57]$ ; IV:  $1.70 + 0.25 + 1.32 + 1.08 + 0.62 = [4.97]$ ; Palp:  $0.29 + 0.11 + 0.10 + (\text{absent}) + 0.38 = [0.88]$ . Abdomen unsclerotized except between epigastric furrow and pedicle. Palp (Figs. 16, 17, 22–24) with cymbial RMP short, narrow, pointed, PC a narrow hook in lateral view; tegulum apex low, smooth, TL small, convex, with small oval denticulate patch; C large, smooth, with small, narrow basal article.

**Variation:** ( $n = 3$ ) Total length 2.18–2.66; ratios of carapace length/width 1.50–1.61, height/width 0.48–0.51; ratios of PER/OQP 2.56–2.69, PER/OAL 2.05–2.10, OQP/OQA 0.83–1.00, PM-PL distance/PM diameter 1.50–1.82, diameter AM/PM 1.17–1.33; ratios of clypeal height/diameter AM 2.12–2.86, cheliceral length/clypeal height 1.84–2.05; ratio of sternum length/width 1.04–1.09; ratio of femur I length/carapace width 4.00–4.65. Dorsal longitudinal bands of abdomen narrow to broad, separate from to confluent with lateral longitudinal bands.

**Female (paratype):** Total length 2.85. Markings and structure as in male (Fig. 38). Carapace 1.05 long, 0.68 wide, 0.30 high; PER and AER 0.44 wide, OAL 0.20; ratio AM:AL:PM:PL,

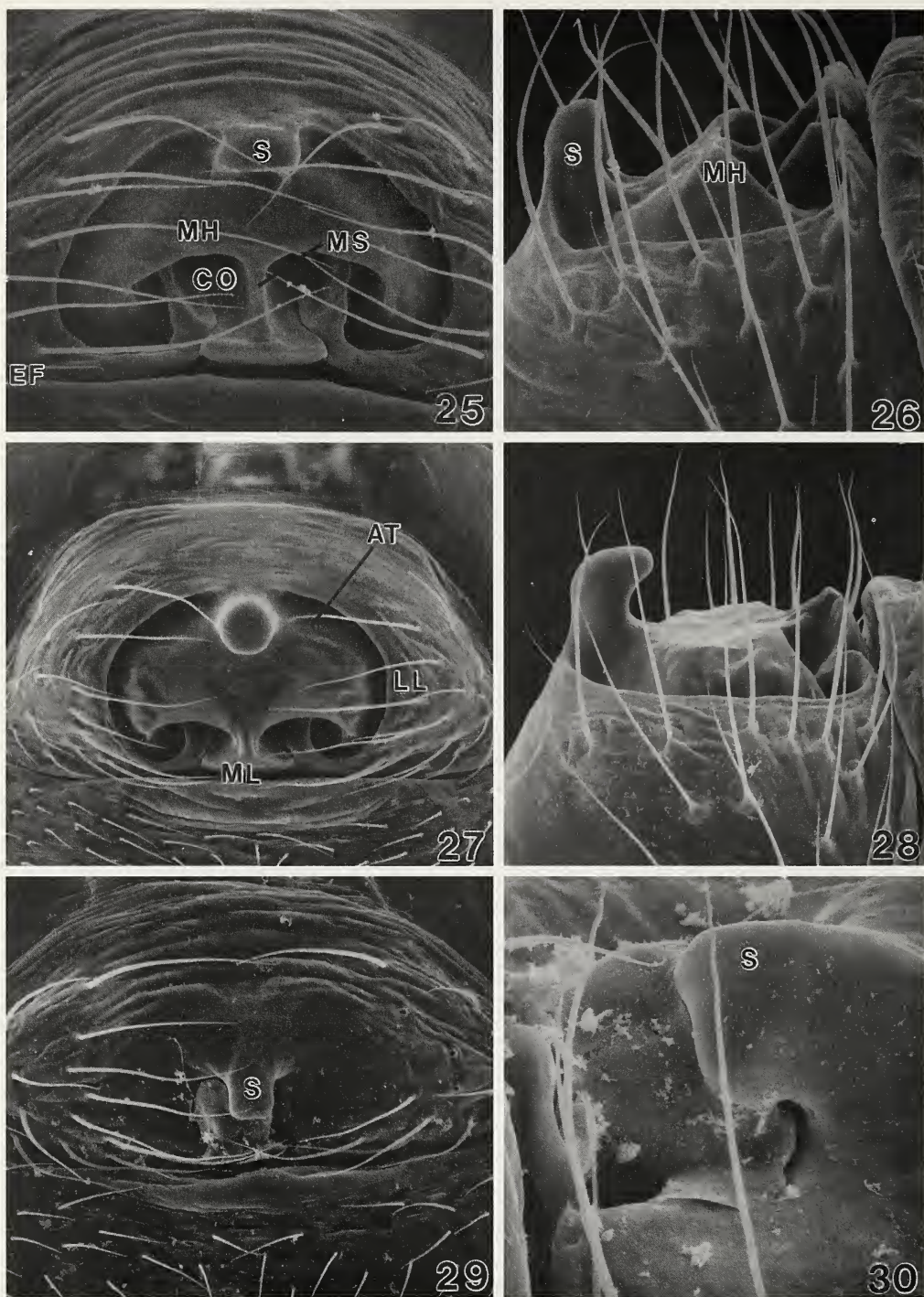
1.6:1.0:1.0:1.08, PM diameter 0.05. Clypeus 0.13 high, chelicerae 0.39 long. Sternum 0.61 long, 0.55 wide; labium 0.11 long, 0.20 wide; palpal coxae 0.21 long, 0.17 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $2.72 + 0.30 + 2.45 + 2.21 + 1.08 = [8.76]$ ; II:  $2.00 + 0.25 + 1.57 + 1.40 + 0.85 = [6.07]$ ; III:  $1.02 + 0.23 + 0.74 + 0.74 + 0.53 = [3.26]$ ; IV:  $1.59 + 0.28 + 1.23 + 1.02 + 0.57 = [4.69]$ ; Palp:  $0.23 + 0.10 + 0.14 + (\text{absent}) + 0.34 = [0.81]$ . Epigynum as in Figs. 18, 25, 26, MS slender, atrial furrows end at S; vulva as in Fig. 35, hyaline AD having small anteromedian fold, large anterior fold, and three small lateral folds before joining HS.

**Variation:** ( $n = 3$ ). Total length 2.25–3.28; ratios of carapace length/width 1.49–1.54, height/width 0.45–0.49; ratios of PER/OQP 2.60–2.80, PER/OAL 2.11–2.33, OQP/OQA 0.88–0.94, PM-PL distance/PM diameter 1.64–1.80, diameter AM/PM 1.60–1.80; ratios of clypeal height/diameter AM 1.22–1.55, cheliceral length/clypeal height 3.08–3.18; ratio of sternum length/width 1.04–1.11; ratio of femur I length/carapace width 3.36–3.94. Dorsal longitudinal bands of abdomen narrow to broad, separate from to confluent with lateral longitudinal bands.

**Natural History.**—These spiders were common in wet montane forest. Individuals built sheet webs in low vegetation, rarely more than 30–40 cm from the forest floor.

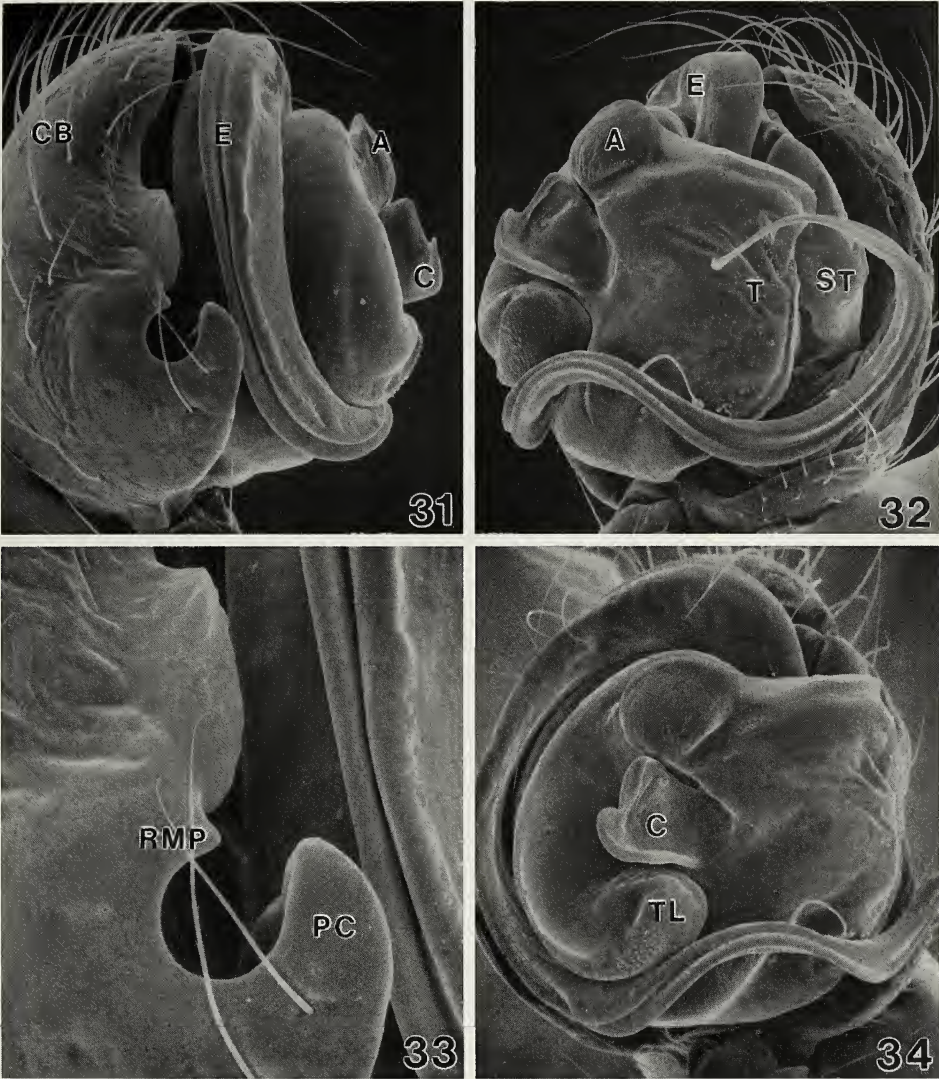
**Distribution.**—Known only from the type locality, an isolated montane rain forest in northern Madagascar (Fig. 98).





Figures 25–30.—Epigyna of Cyatholipidae. 25, 27, 29. Ventral view; 26, 28, 30. Lateral view; 25, 26. *Ulwembua antsiranana* new species, Montagne d'Ambre; 27, 28. *Ulwembua ranomafana* new species, paratype; 29, 30. *Vazaha toamasina* new species, paratype. AT = atrium; CO = copulatory openings; EF = epigastric furrow; LL = lateral lobes; MH = median hood; ML = median lobe; MS = median septum; S = scape.





Figures 31–34.—Right male palpus of *Ulwembua ranomafana* new species, holotype. 31. Retrolateral view; 32. Proventral view; 33. Cymbial base, retrolateral view; 34. Ventral view. A = apical lobe of tegulum; C = conductor; CB = cymbium; E = embolus; PC = paracymbium; RMP = retromedian cymbial process; ST = subtegulum; T = tegulum; TL = ventromedian tegular lobe.

**Additional material examined.**—**MADAGASCAR:** *Antsiranana Province:* Parc National Montagne d'Ambre, 2.79 air km NE of park entrance, forest, (12°32'S, 49°10'E), elev. approx. 1000 m, 21–30 November 1993 (N. Scharff, C. Griswold, J. Coddington, S. Larcher and R. Andriamasamana), 31♂67♀, one pair in MRAC, remainder in CAS, USNM, and ZMUC.

*Ulwembua ranomafana* new species

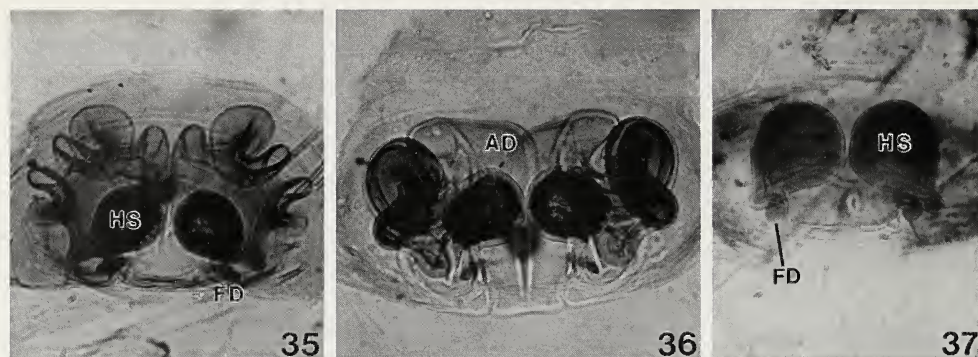
Figs. 15, 19–21, 27, 28, 31–34, 36, 39, 98

**Types.**—Male holotype and female paratype from forest at approximately 1100 m elevation at Vohiparara, Parc National de Ranomafana, Fianarantsoa Province, Madagascar, 7 December 1993, C. Griswold (CAS).

**Etymology.**—The type locality, a noun in apposition to the generic name.

**Diagnosis.**—Carapace dark except along lateral margins and on central longitudinal band extending from PM posteriorly to behind thoracic fovea (Fig. 39). Male with E weakly sinuate across tegulum base, C simple, median, longitudinal (Figs. 20, 34). Vulva with AD simpler than in *U. antsiranana* (Fig. 36).





Figures 35–37.—Vulvae of Cyatholipidae, dorsal view, cleared. 35. *Ulwembua antsiranana* new species, Montagne d'Ambre; 36. *U. ranomafana* new species, paratype; 37. *Vazaha toamasina* new species, paratype. AD = afferent duct; FD = fertilization duct; HS = spermathecal head.

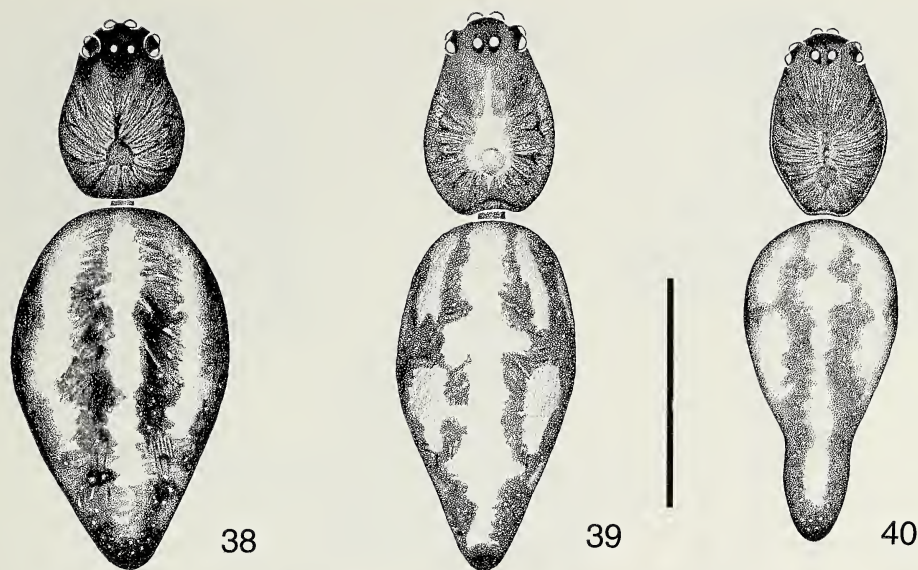
**Description.**—*Male (holotype)*: Total length 2.47. Carapace yellow-white, with broad dark gray dorsolateral bands extending from margins of pars cephalica to posterior margin, leaving narrow yellow-white band along lateral margin and broad central yellow-white band from pars cephalica to thoracic fovea; ocular area with black surrounding and extending between AM and extending posteriorly to surround each PM, and surrounding and extending between lateral eyes; clypeus yellow-brown, dark in center from AM to oral margin; chelicerae dark brown, palpal coxae, labium and sternum nearly black; coxae, trochanters, basal segments of palpi and bases of leg femora yellow-white, cymbium dark brown, legs shading distally to yellow-brown, unmarked except that apices of femora and tibiae are lighter; abdomen white, with black dorsolateral bands meeting posteriorly, each band encompasses narrow anterior and median oval white spots, venter gray, black from spinnerets to pedicel. Carapace 1.24 long, 0.80 wide, 0.36 high, texture finely granulate becoming denticulate posteriorly, posterior margin truncate, thoracic fovea a deep oval; PER 0.47 wide, AER 0.46 wide, OAL 0.22; ratio AM:AL:PM:PL, 1.23:1.08:1.0:1.23, PM diameter 0.07. Clypeus 0.18 high, chelicerae 0.37 long, with basal projection. Sternum 0.61 long, 0.55 wide, rugose; labium 0.11 long, 0.20 wide; palpal coxae 0.21 long, 0.17 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $3.74 + 0.34 + 3.51 + 3.72 + 1.49 = [12.80]$ ; II:  $2.47 + 0.30 + 1.94 + 2.04 + 0.96 = [7.71]$ ; III:  $0.96 + 0.21 + 0.79 + 0.79 + 0.49 = [3.24]$ ; IV:

$1.59 + 0.25 + 1.23 + 1.06 + 0.53 = [4.66]$ ; Palp:  $0.35 + 0.13 + 0.10 + (\text{absent}) + 0.40 = [0.98]$ . Abdomen unsclerotized except strongly between epigastric furrow and pedicel. Palp (Figs. 20, 21, 31–34) with cymbial RMP blunt, very short, PC broad in lateral view; tegulum apex bulging, smooth, TL small, denticulate in elongate oval patch; C simple.

*Female (paratype)*: As in Figs. 15, 39. Total length 2.85. Markings and structure as in male except dorsal light marking of carapace broader, black dorsolateral bands of abdomen encompassing broad lateral white spots, anterior white spots confluent with median white band, venter gray. Carapace 1.05 long, 0.68 wide, 0.30 high, thoracic fovea a shallow oval; PER and AER 0.44 wide, OAL 0.20; ratio AM:AL:PM:PL, 1.6:1.2:1.0:1.3, PM diameter 0.05. Clypeus 0.13 high, chelicerae 0.39 long, with weak basal projection. Sternum 0.61 long, 0.55 wide; labium 0.11 long, 0.20 wide; palpal coxae 0.21 long, 0.17 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $2.51 + 0.28 + 2.13 + 2.13 + 1.04 = [8.09]$ ; II:  $1.55 + 0.23 + 1.13 + 1.21 + 0.70 = [4.82]$ ; III:  $0.79 + 0.17 + 0.51 + 0.45 + 0.42 = [2.34]$ ; IV:  $1.28 + 0.23 + 0.91 + 0.79 + 0.49 = [2.34]$ ; Palp:  $0.24 + 0.10 + 0.13 + (\text{absent}) + 0.33 = [0.80]$ . Epigynum as in Figs. 19, 27, 28; MS between CO broad, atrial furrows end just behind S; vulva as in Fig. 36, hyaline AD having broad anteromedian chamber and forming large lateral and posterolateral folds before joining HS.

*Variation*: ( $n = 3$ ). Total length 2.72–3.19;





Figures 38–40.—Female Cyatholipidae, dorsal views. 38. *Ulwembua antsiranana* new species, Montagne d'Ambre; 39. *U. ranomafana* new species, paratype; 40. *Vazaha toamasina* new species, paratype. (Scale bar = 1 mm)

ratios of carapace length/width 1.39–1.50, height/width 0.38–0.50; ratios of PER/OQP 2.35–2.62, PER/OAL 1.95–2.21, OQP/OQA 0.89–1.00, PM-PL distance/PM diameter 1.07–1.33, diameter AM/PM 1.14–1.50; ratios of clypeal height/diameter AM 1.44–1.50, cheliceral length/clypeal height 2.61–3.00; ratio of sternum length/width 1.00–1.14; ratio of length femur I/carapace width 3.57–3.71.

**Distribution.**—Known only from the type locality in montane rain forest (Fig. 98).

**Additional material examined.**—MADAGASCAR: Fianarantsoa Province: Parc National de Ranomafana, Vohiparara, ca. 21°14'S, 47°24'E, elev. 1100 m, 5–7 November 1993 (N. Scharff, S. Larcher, C. Griswold, and R. Andriamasamanana) 2♀ (ZMUC, USNM).

#### *Vazaha* new genus

**Type species.**—*Vazaha toamasina* new species

**Etymology.**—From the Malagasy for forerunner; gender feminine.

**Diagnosis.**—Female epigynum (Figs. 29, 30, 43) with S but lacking MH, male palp with cymbial RMP directed distad (Figs. 45, 48); E thick, lacking PP.

**Description.**—See under species description below of *Vazaha toamasina* new species.

**Composition.**—One species.

**Distribution.**—Madagascar (Fig. 98).

#### *Vazaha toamasina* new species

Figs. 29, 30, 37, 40–48, 98

**Types.**—Male holotype and female paratype from forest at an elevation of 1000 m at Parc National Perinét, Toamasina Province, Madagascar, 4–5 November 1993, C. E. Griswold (CAS).

**Etymology.**—From the home province, a noun in apposition to the generic name.

**Diagnosis.**—See generic diagnosis above.

**Description.**—*Male (holotype)*: As in Figure 41. Total length 2.38. Carapace dusky yellow-brown, pale yellow-brown in center behind pars cephalica surrounding thoracic fovea, ocular area dusky, dark grey surrounding AME; clypeus and chelicerae dusky grey-brown, unmarked, palpal coxae, labium and sternum dark grey-brown; coxae and trochanters white, legs shading from white at base to pale yellow-brown from distal femora to tarsi, palpi white except for grey-brown cymbium; abdomen pale grey, dorsum with median pair of longitudinal dark bands that meet posteriorly outlining median white area and laterally outlining an anterior and median light longitudinal spot, venter dark grey from pedicel to beyond spinnerets, weakly sclerotized ventrally between pedicel and epigastric furrow,

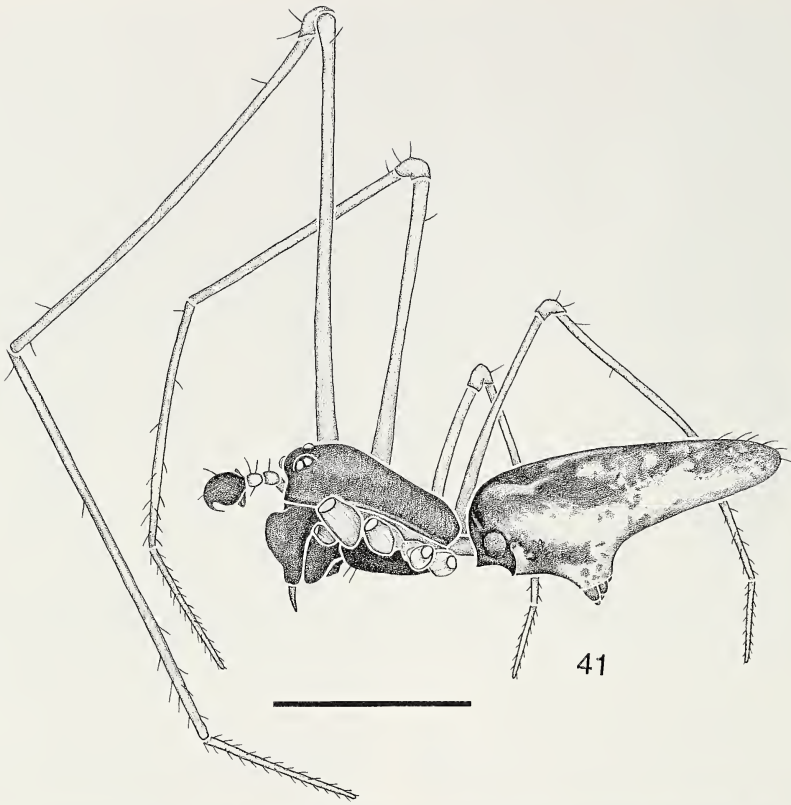


Figure 41.—*Vazaha toamasina* new species, holotype male, lateral view. (Scale bar = 1 mm)

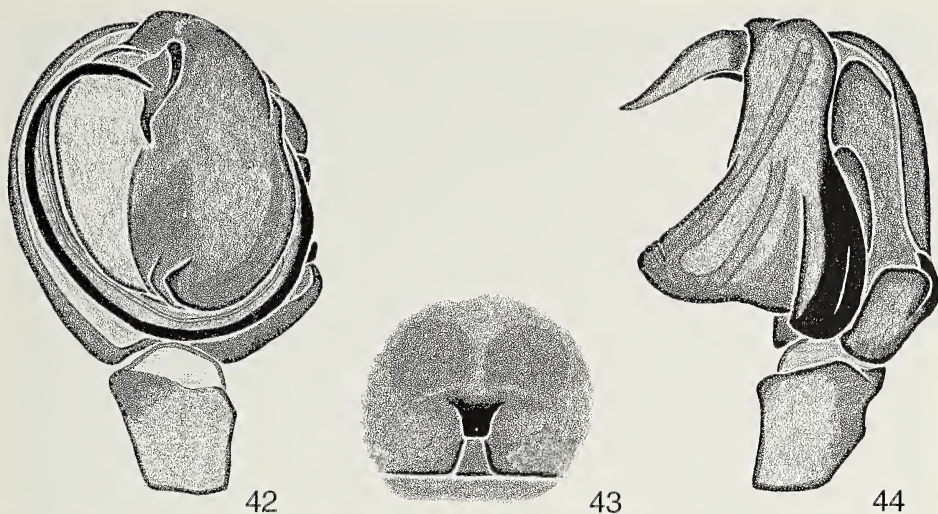
otherwise unsclerotized, abdominal setae fine, with small setal base picks on anterior margin. Carapace 1.09 long, 0.68 wide, 0.35 high, oval in dorsal view, posterior margin weakly concave, finely rugose, thoracic fovea a shallow oval; PER and AER 0.43 wide, OAL 0.20; ratio AM:AL:PM:PL, 1.0:1.33:1.0:0.92, PM diameter 0.06. Clypeus 0.16 high, chelicerae 0.46 long, with large antieriad-directed basal projection. Sternum 0.60 long, 0.55 wide, finely granulate; labium 0.11 long, 0.18 wide; palpal coxae 0.21 long, 0.16 wide; leg coxae surrounded by unsclerotized cuticle. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $2.64 + 0.23 + 2.38 + 2.36 + (\text{missing}) = [?]$ ; II:  $1.94 + 0.25 + 1.59 + 1.57 + 0.81 = [6.16]$ ; III:  $0.89 + 0.21 + 0.68 + 0.68 + 0.47 = [2.93]$ ; IV:  $1.42 + 0.23 + 1.00 + 1.00 + 0.49 = [4.14]$ ; Palp:  $0.33 + 0.13 + 0.08 + (\text{absent}) + 0.26 = [0.80]$ . Palp (Figs. 42, 44–48) with cymbial RMP short, narrow, directed distad, PC broad and blunt in lateral view; tegulum apex a small, pointed lobe, TL pointed, weakly wrin-

kled; C a distal, simple, elongate basad-directed triangle; E stout, arising near 2 o'clock, PP absent.

*Female (paratype)*: As in Fig. 40. Total length 2.21. Markings as in male. Carapace 1.01 long, 0.70 wide, 0.31 high; PER 0.40 wide, AER 0.38 wide, OAL 0.19; ratio AM:AL:PM:PL, 1.17:1.0:1.0:1.0, PM diameter 0.06. Clypeus 0.11 high, chelicerae 0.39 long, with small antieriad-directed basal projection. Sternum 0.59 long, 0.51 wide, texture nearly smooth; labium 0.14 long, 0.18 wide; palpal coxae 0.21 long, 0.15 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $2.29 + 0.25 + 1.91 + 1.91 + 0.91 = [7.27]$ ; II:  $1.62 + 0.28 + 1.28 + 1.28 + 0.72 = [5.18]$ ; III:  $0.74 + 0.21 + 0.57 + 0.57 + 0.42 = [2.51]$ ; IV:  $1.28 + 0.21 + 0.96 + 0.81 + 0.47 = [3.73]$ ; Palp:  $0.25 + 0.08 + 0.11 + (\text{absent}) + 0.28 = [0.72]$ . Epigynum as in Figs. 29, 30, 43, with S but lacking MH; vulva as in Fig. 37, CO lead directly to large, sclerotized HS, AD absent.

*Variation*: ( $n = 2$ ). Total length 2.21–2.81;





Figures 42-44.—Genitalia of *Vazaha toamasina* new species. 42, 44. Left male palpus, holotype; 43. Epigynum, paratype; 42, 43. Ventral view; 44. Retrolateral view.

ratios of carapace length/width 1.43–1.51, height/width 0.43–0.45; ratios of PER/OQP 2.53–2.78, PER/OAL 2.11–2.17, OQP/OQA 0.87–1.00, diameter AM/PM 1.17–1.45; ratios of clypeal height/diameter AM 1.25–1.57, cheliceral length/clypeal height 3.36–4.00; ratio of length femur I/carapace width 3.22–3.35.

**Distribution.**—Known only from the type locality on the eastern escarpment in central Madagascar (Fig. 98).

**Additional material examined.**—MADAGASCAR: *Toamasina Province*, Parc National Perinét, near Andasibe, 18°56'S, 48°24'E, elev. 1000 m, 4–5 November 1993 (C. Griswold) 2♀ (CAS).

#### *Alaranea* new genus

**Type species.**—*Alaranea merina* new species.

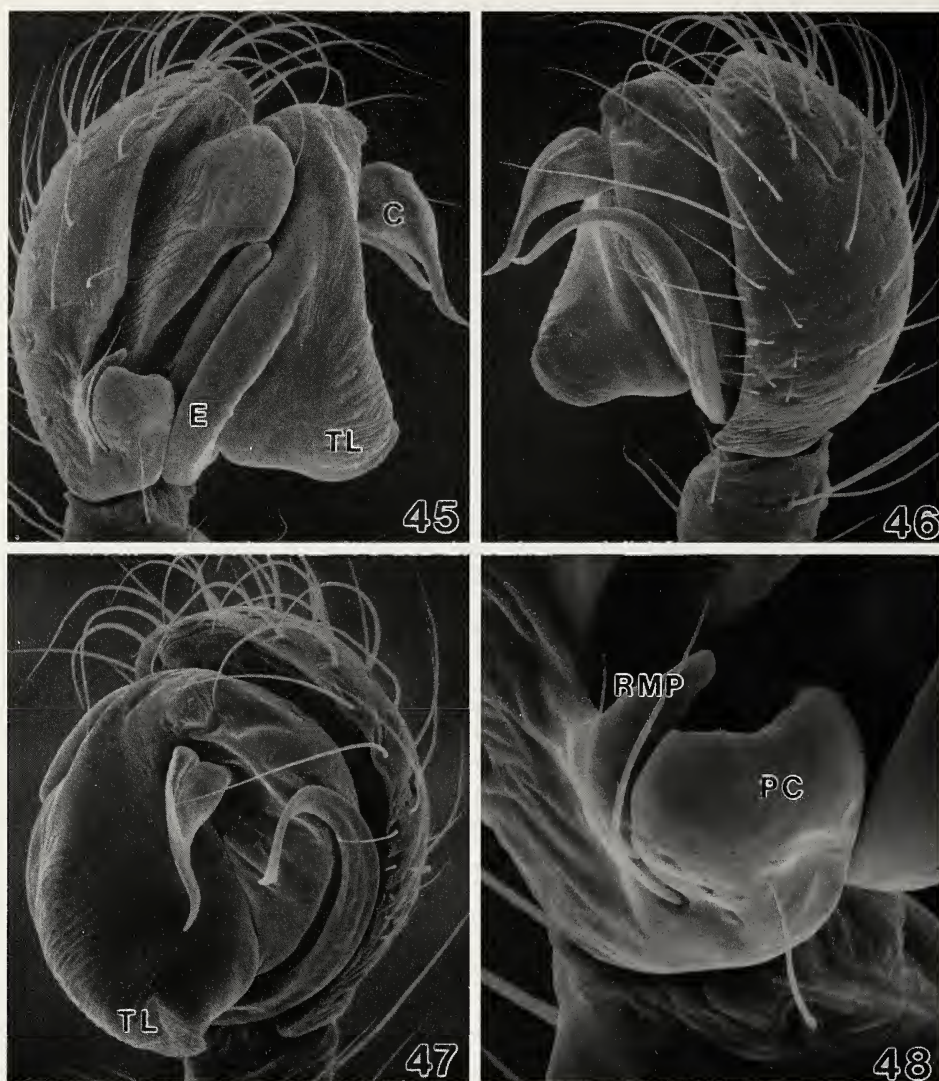
**Etymology.**—Combination of Malagasy Ala, and Latin Aranea, both meaning spiders, considered feminine.

**Diagnosis.**—Anterior portion of abdomen of both sexes forming a sclerotized, annulate petiole produced dorsally into a short projection or horn (Figs. 4, 66, 94); abdomen of males with a thin, shiny transparent dorsal scutum (Fig. 95); PP present (Figs. 53, 57, 73, 89).

**Description.**—Total length 1.60–3.00. Carapace of most species narrowly trapezoidal in dorsal view (Figs. 63, 66, 95, 96), oval in *A. alba* new species (Fig. 69), length 1.39–1.67

times width, low, maximum height 0.38–0.52 width; texture finely rugose (Fig. 50), thoracic fovea a small, round pit, carapace posterior margin weakly concave medially, forming weakly upturned lip; ocular area with PER width 1.83–2.56 times OAL, 2.14–2.69 times OQP, OQP 0.81–1.11 times OQA; diameter AM 1.00–1.60 times PM, distance PM-PL 0.80–1.50 times PM diameter; clypeal height 1.11–2.40 times AM diameter, cheliceral length 1.93–3.80 times clypeal height (Fig. 51); chelicerae unmodified. Sternum rugose (Fig. 49) to pustulate, length 0.88–1.15 times width, plural and sternal sclerotizations extend between and surround coxae (Figs. 2, 68, 94). Abdomen sclerotized from epigastric furrow to and surrounding pedicel (Figs. 63–69), sclerotization forming annulate petiole produced dorsally into a short projection or horn (Figs. 4, 94), anterior sclerotization much broader in males, males with a thin, shiny transparent dorsal scutum (Fig. 95), abdomen otherwise unsclerotized, oval to triangular; abdominal setae short, slender, bases of anterior setae unmodified. Legs short, femur I length 1.63–2.11 times carapace width, unmodified (Figs. 68, 94). Male palpus (Figs. 57–62) with cymbial RMP pointing ventrad, smaller than PC; palpal bulb with dentate TL, apex a small, smooth to pustulate lobe; C median, longitudinal, simple or with accessory process, smooth or rarely dentate; E thick, making sim-





Figures 45–48.—*Vazaha toamasina* new species, holotype male, right palpus. 45. Retrolateral view; 46. Prolateral view; 47. Ventral view; 48. Cymbial base, retrolateral view. C = conductor; E = embolus; PC = paracymbium; RMP = retromedian cymbial process; TL = ventromedian tegular lobe.

ple curve, origin apical between 10–11 o'clock, ridged; PP present, fleshy, pustulate, with or without teeth, thick or hooked apically; sperm duct with tight double twist (curl-cue) near embolic base. Epigynum (Figs. 55, 56, 74–77) with S and long MH with slender MS between CO, ML parallel-sided. Vulva (Figs. 90–93) with sclerotized, simple hemispherical lateral AD, in most specimens larger than HS, FD posterior.

**Composition.**—Four species.

**Distribution.**—Madagascar (Fig. 98).

*Alaranea betsileo* new species

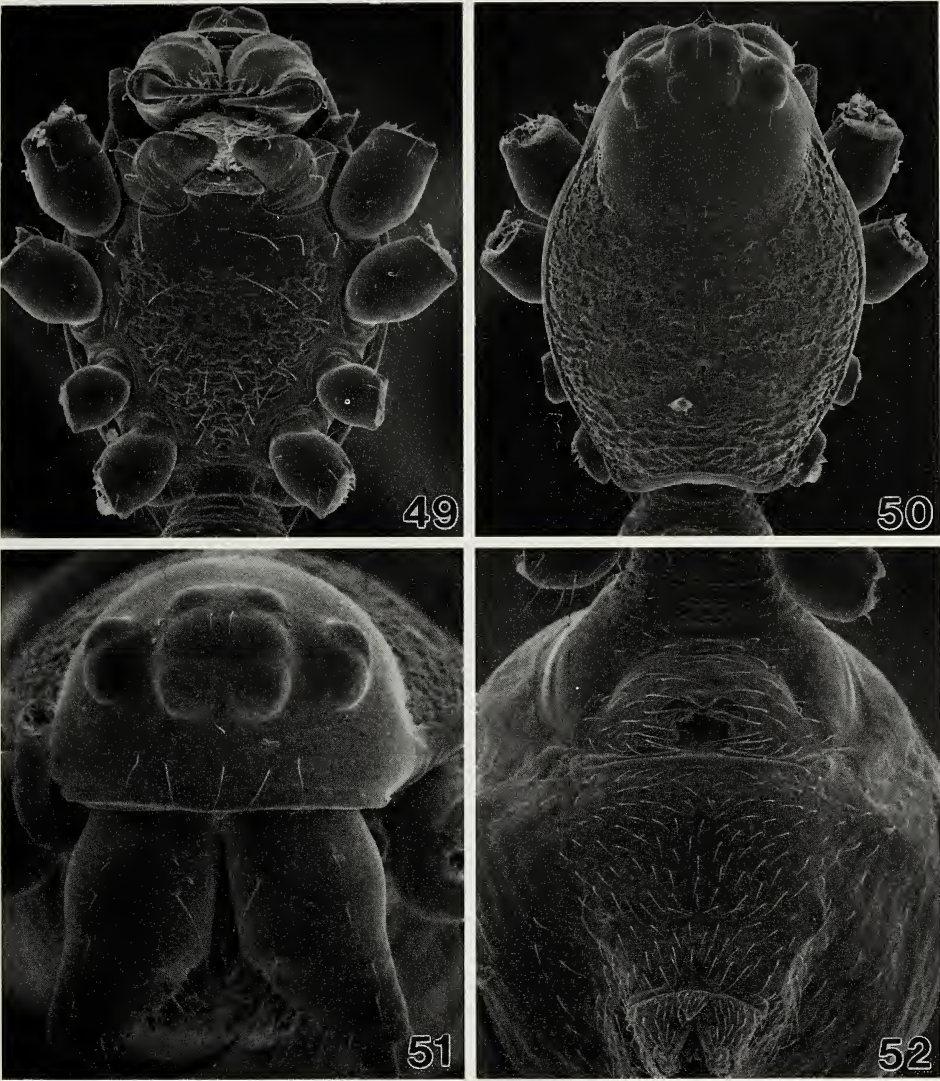
Figs. 2–4, 6–14, 49–54, 56, 59–64, 74, 75, 90, 98

**Types.**—Male holotype and female paratype from Madagascar, Fianarantsoa Province, Parc National Ranomafana, Talatakely, montane rain forest, 21°15'S, 47°25'E, elev. 900 m, 5–7 November 1993 (C. Griswold) (CAS).

**Etymology.**—Named for the indigenous people of Fianarantsoa Province.

**Diagnosis.**—Conductor bipartite, with thin, broad proximal piece separate from C proper





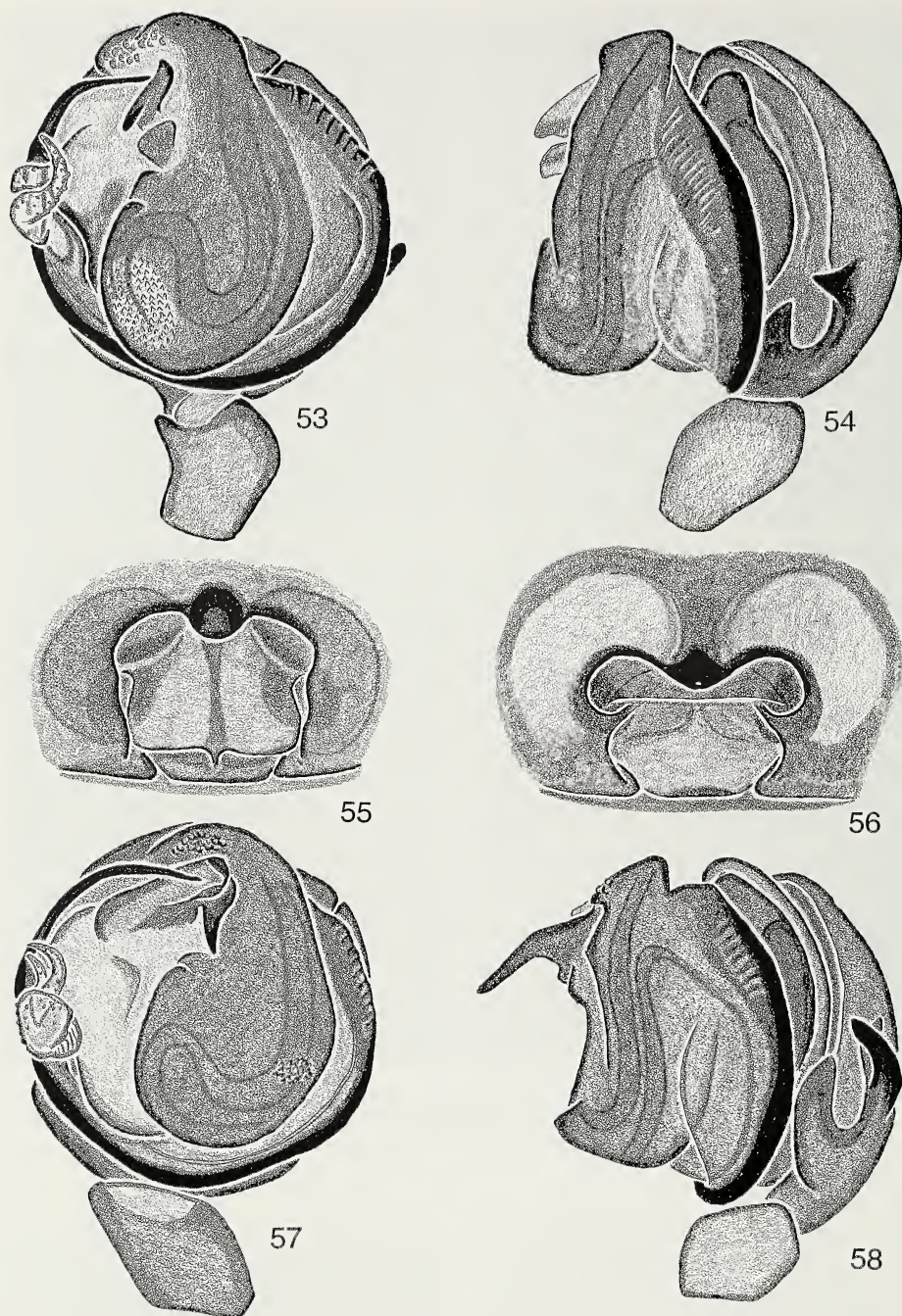
Figures 49–52.—Morphology of *Alaranea betsileo* new species, from Talatakely. 49. Carapace, ventral view; 50. Carapace, dorsal view; 51. Carapace, anterior view; 52. Abdomen, ventral view; 49, 50. Male; 51, 52. Female.

(Figs. 53, 61); in both sexes sternum dark red-brown to black, abdomen of most specimens with extensive dark markings, dorsum lacking sinuate longitudinal dark bands, with median black band surrounding 1–2 anterior white spots (Figs. 63, 64).

**Description.**—*Male* (7 km W Ranomafana): Total length 2.24. Carapace dark red-brown, unmarked, ocular area with diffuse dark grey surrounding AM, black surrounding AL-PL; clypeus dusky grey in center, chelicerae red-brown, with faint dark anterobasal streaks; palpal coxae red-brown, lighter at

tips; labium and sternum dark brown to nearly black; coxae, legs, and palpi yellow-white, unmarked, cymbium dusky yellow-brown; abdomen black dorsally beneath shiny transparent scutum, dark transverse bands extending laterally from midpoint and posterior, those in middle nearly meeting ventrally, dark brown sclerotization extending from epigastric furrow to and surrounding pedicel to form annulate petiole, sclerotization very broad anterodorsally. Carapace 1.04 long, 0.64 wide, 0.26 high, trapezoidal in dorsal view; PER 0.38 wide, AER 0.39 wide, OAL 0.19; ratio AM:



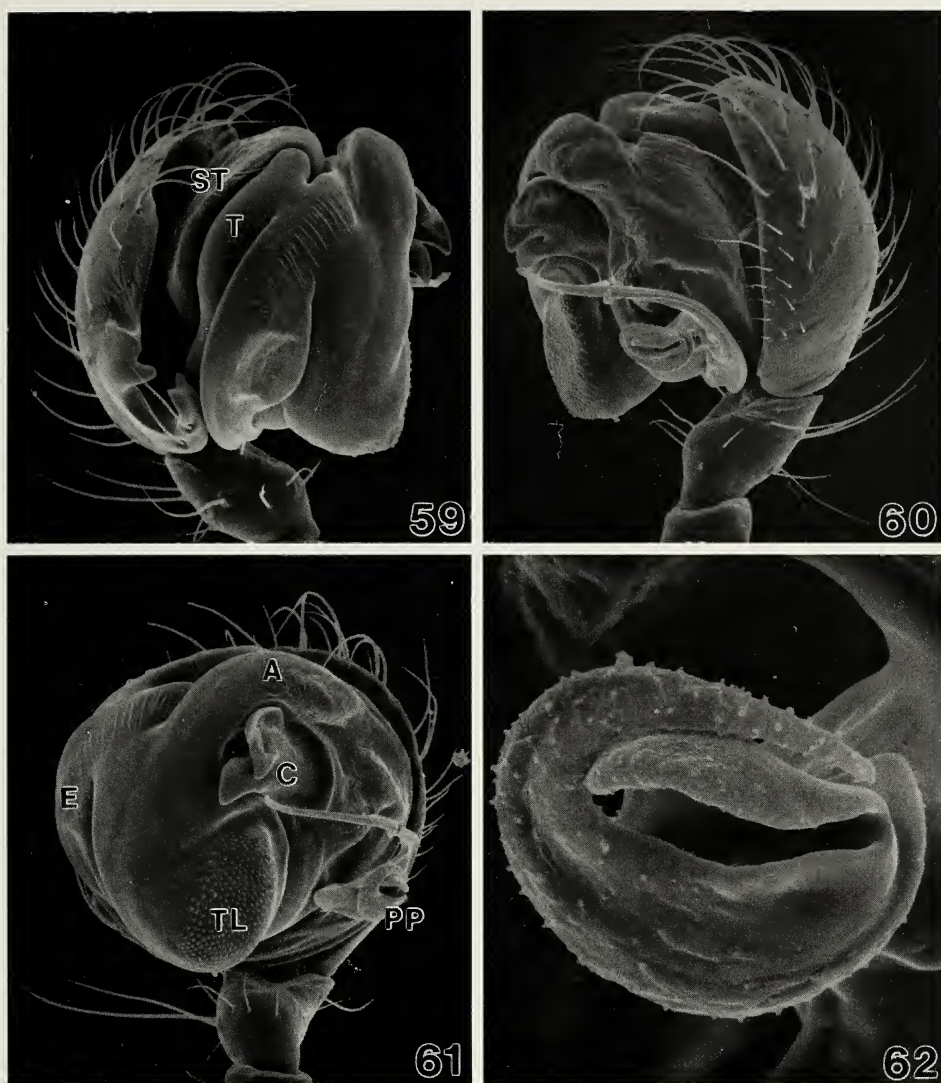


Figures 53–58.—Genitalia of *Alaranea* spp. 53, 54, 57, 58. Left male palpus; 55, 56. Epigynum; 53, 55–57. Ventral view; 54, 58. Retrolateral view; 53, 54, 56. *Alaranea betsileo* new species, from 7 km W Ranomafana; 55. *A. alba* new species, paratype; 57, 58. *A. alba* new species, holotype.

AL:PM:PL, 1.33:1.0:1.0:1.0, PM diameter 0.06. Clypeus 0.14 high, chelicerae 0.33 long. Sternum 0.50 long, 0.50 wide; labium 0.10 long, 0.14 wide; palpal coxae 0.16 long, 0.12

wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I: 2.60 + 0.42 + 2.08 + 2.20 + 1.36 = [8.66]; II: 2.32 + 0.40 + 2.32 + 1.96 + 1.28 = [8.28];





Figures 59–62.—*Alaranea betsileo* new species, male from Talatakelo, right palpus. 59. Retrolateral view; 60. Prolateral view; 61. Ventral view; 62. Parembolic process. A = apical lobe of tegulum; C = conductor; E = embolus; PP = parembolic process; ST = subtegulum; T = tegulum; TL = ventromedian tegular lobe.

III:  $1.48 + 0.36 + 1.48 + 1.04 + 0.80 = [5.16]$ ; IV:  $2.20 + 0.40 + 1.72 + 1.56 + 0.88 = [6.76]$ ; Palp:  $0.28 + 0.10 + 0.09 + (\text{absent}) + 0.24 = [0.71]$ . Palp (Figs. 53, 54, 59–62) with cymbial RMP short, acutely pointed, with distal blunt projection, PC broad in lateral view; tegulum apex pustulate, TL large, convex, dentation extensive; C large, double, with flattened translucent lower article nearly as large as C proper; PP with apical recurved hook.

Variation: ( $n = 3$ ). Total length 2.12–2.61;

ratios of carapace length/width 1.54–1.62, height/width 0.39–0.42; ratios of PER/OQP 2.37–2.53, PER/OAL 1.85–2.16, OQP/OQA 0.88–0.94 distance PM-PL/diameter PM 1.14–1.40, diameter AM/PM 1.00–1.60; ratios of clypeal height/AM diameter 1.62–1.86, cheliceral length/clypeal height 2.36–2.46; ratio of sternum length/width 0.88–1.00; ratio of length femur I/carapace width 1.87–2.07. Markings of carapace dark brown to nearly black; legs pale yellow white to dusky gray; abdomen with dorsolateral transverse

marks entire to broken to rarely absent, dorsal black area ranges from narrow median band to totally covering dorsum.

**Female** (7 km. W Ranomafana): Total length 2.24. Carapace red-brown, dusky on pars cephalica and around thoracic fovea, with median yellow-brown area between thoracic fovea and posterior margin of pars cephalica, ocular area dark grey between AM-PM and AL-PL, dusky marking extending below AM to lower margin of clypeus; chelicerae and palpal coxae yellow-brown, unmarked; labium and sternum dark brown to black; coxae, legs, and palpi yellow-white, unmarked; abdomen yellow-white, dorsum with broad longitudinal black mark, this mark forming lateral transverse bands near middle, small black spot at posterior apex, venter yellow-white, unmarked; dark brown sclerotization extending from epigastric furrow to and surrounding pedicel to form annulate petiole, sclerotization much less extensive anteriorly than in male. Carapace 0.94 long, 0.60 wide, 0.25 high; PER 0.37 wide, AER 0.36 wide, OAL 0.18; ratio AM:AL:PM:PL, 1.6:1.2:1.0:1.2, PM diameter 0.06. Clypeus 0.11 high, chelicerae 0.28 long. Sternum 0.50 long, 0.47 wide; labium 0.10 long, 0.16 wide; palpal coxae 0.17 long, 0.12 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $2.24 + 0.44 + 1.80 + 1.72 + 1.06 = [7.26]$ ; II:  $2.00 + 0.42 + 1.60 + 1.48 + 1.02 = [6.52]$ ; III:  $1.24 + 0.36 + 0.92 + 0.84 + 0.76 = [4.12]$ ; IV:  $1.84 + 0.40 + 1.36 + 1.20 + 0.78 = [5.58]$ ; Palp:  $0.21 + 0.09 + 0.11 + (\text{absent}) + 0.22 = [0.63]$ . Epigynum as in Figs. 56, 74, 75; vulva as in Fig. 90.

**Variation:** ( $n = 3$ ). Total length 2.18–2.89; ratios of carapace length/width 1.56–1.69, height/width 0.34–0.43; ratios of PER/OQP 1.91–2.30, PER/OAL 1.28–2.00, OQP/OQA 0.80–1.00, distance PM-PL/PM diameter 1.28–2.00, diameter AM/PM 1.14–1.67; ratios of clypeal height/AM diameter 1.40–2.00, cheliceral length/clypeal height 2.22–3.71; ratio of sternum length/width 1.03–1.10; ratio of length femur I/carapace width 1.92–2.17. Carapace of most specimens dark brown to black, in rare specimens orange-brown, unmarked; dorsal abdominal dark markings range from narrow, broken laterally (Fig. 63) to broad, almost obscuring dorsum (Fig. 64), anteromedian white spot rarely obscure.

**Natural history.**—Common inside forest

hanging beneath sheet webs between 0.2–2 m above ground.

**Distribution.**—Known only from montane forests near Ranomafana in Fianarantsoa Province (Fig. 98).

**Material examined.**—**MADAGASCAR:** *Fianarantsoa Province:* Parc National Ranomafana, Talatakely, montane rain forest, 21°15'S, 47°25'E, elev. 900 m, 34♂74♀ (including holotype and paratype), 5–7 November 1993 (N. Scharff, S. Larcher, C. Griswold, and R. Andriamasamanana) (one pair in MRAC, remainder divided among CAS, USNM, and ZMUC). Parc National Ranomafana, Vohiparara, 21°14'S, 47°24'E, elev. 900 m, 6♂6♀, 5–7 December 1993 (N. Scharff, S. Larcher, C. Griswold, and R. Andriamasamanana) (CAS, ZMUC, USNM); Parc National Ranomafana, 200 m N research Cabin, trail G, beating, 1♂2♀ (CAS) 2♂2♀ (MCZ), 23 March 1992 (S. Kariko, V. Roth); Parc National Ranomafana, beating in forest, 1♂4♀ (CAS), 4♂12♀ (MCZ), 25 March 1992 (Emile); Parc National Ranomafana, 200 m N research Cabin, trail G, beating, 2♂4♀, 25 March 1992 (B. Roth) (CAS); Parc National Ranomafana, 21°12'S, 47°27'E, from foliage, elev. 1000 m, 4♀ (CAS) 3♀ (MCZ) April 1992 (V. & B. Roth); Parc National Ranomafana, 7 km W Ranomafana, elev. 900 m, 21°12'S, 47°27'E, 2♂, 20–24 March 1990, elev. 1100 m, 1♂1♀, 8–21 October 1988, 1♂, 21–30 October 1988, 2♂, 1–7 November 1988 (W. Steiner) (USNM).

#### *Alaranea merina* new species

Figs. 5, 65, 66, 70–73, 76, 77, 91, 98

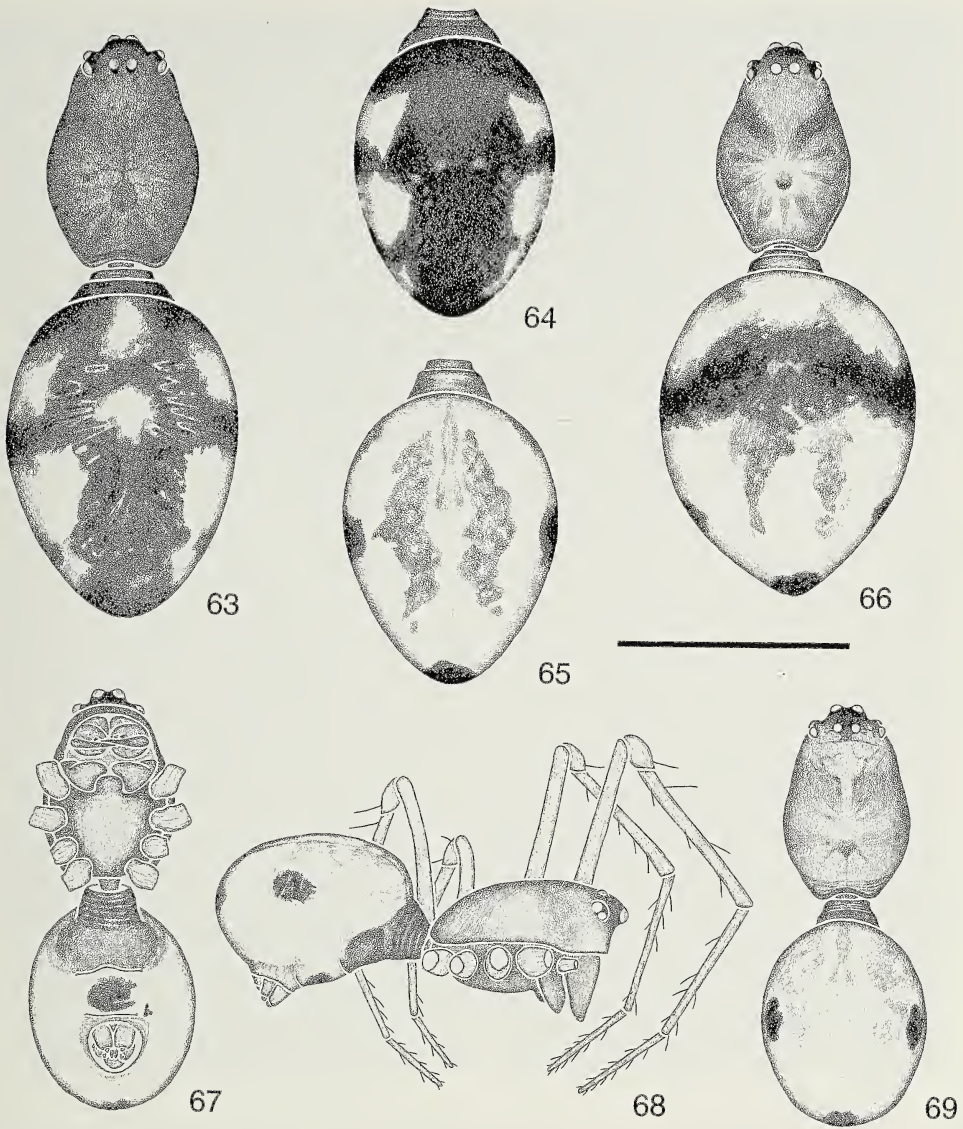
**Types.**—Male holotype and female paratype from Madagascar, Toamasina Province, Parc National Perinét, near Andasibe, 18°56'S, 48°24'E, elev. 1000 m, montane rain forest, 4–5 November 1993 (C.E. Griswold) (CAS).

**Etymology.**—Named for the indigenous people of Antananarive Province.

**Diagnosis.**—Conductor simple, proximal point narrower than cup (Figs. 70–72); dorsum of abdomen with sinuate longitudinal dark bands diverging from apex to middle and converging posteriorly (Figs. 65, 66). There seem to be no consistent characters to separate females of *merina* new species from *ardua* new species, though in the former the carapace is pale yellow-brown with darker markings along the borders of the pars cephalica (Fig. 66), whereas the carapace of *ardua* tends to be darker (Fig. 96).

**Description.**—**Male** (7 km. W Ranomafana): Total length 2.32. Carapace yellow-

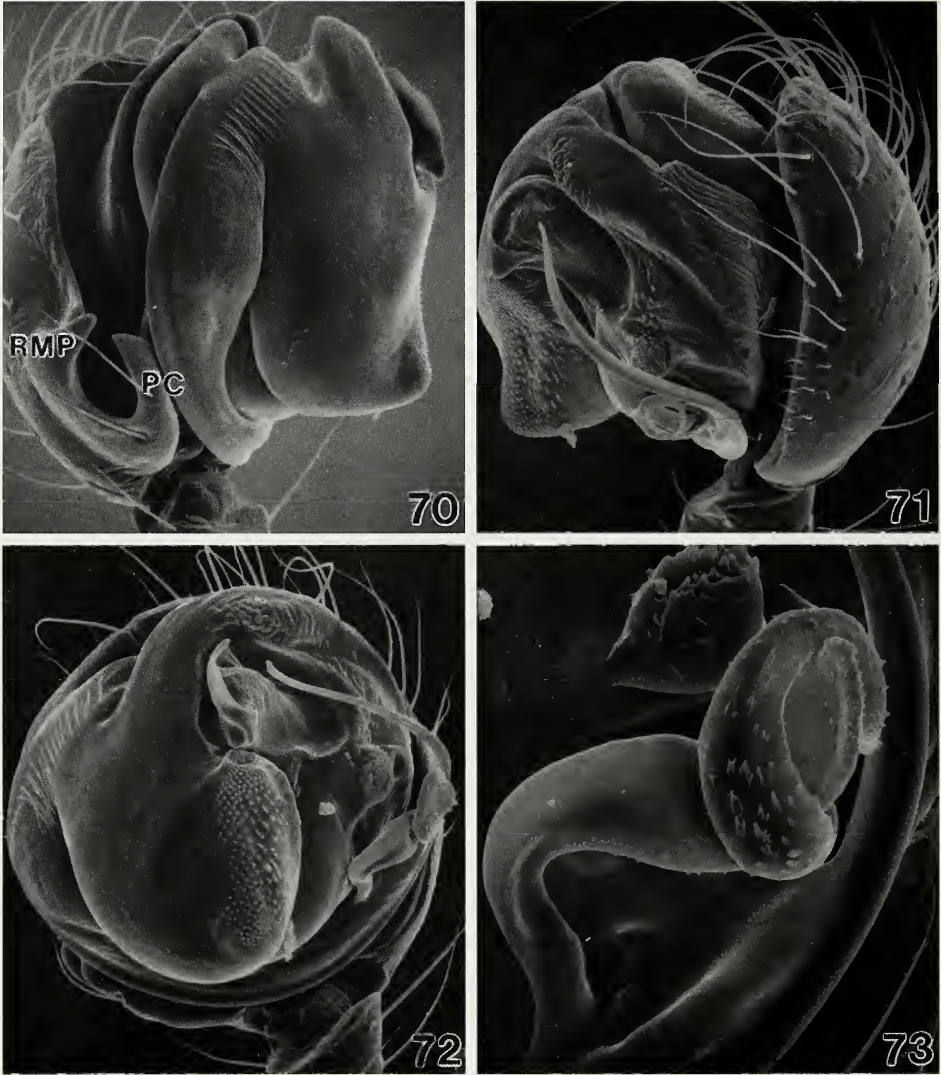




Figures 63–69.—Morphology of *Alaranea* spp. 63–66, 69. Dorsal view, 64 and 65 abdomen only; 67. Ventral view; 68. Lateral view; 63, 64. *Alaranea betsileo* new species, females from Talatakely; 65, 66. *Alaranea merina* new species, females from Perinét; 67–69. *Alaranea alba* new species, holotype male. (Scale bar = 1 mm)

brown, brown along margins of pars cephalica and on thoracic fovea; ocular area dark grey beginning just anterior of PER, black between AM and AL-PL; clypeus yellow-brown, dark grey in center from AM to clypeal margin; chelicerae and palpal coxae orange-brown; sternum and labium black; legs and palpi yellow-white, unmarked, cymbium yellow-brown, tegulum orange-brown; abdomen white, with brown sclerotization extending from epigastric furrow to and surrounding

pedicel to form annulate petiole, dorsum with faint longitudinal brown bands beneath transparent scutum, with dorsolateral elongate black spot and posterior lateral wavy line, posterior apex with black spot, venter dark gray between epigastric furrow and spiracle. Carapace 1.00 long, 0.64 wide, 0.28 high, trapezoidal in dorsal view; PER 0.39 wide, AER 0.38, OAL 0.19; ratio AM:AL:PM:PL 1.5:1.17:1.0:1.17, PM diameter 0.06. Clypeus 0.12 high, chelicerae 0.30 long. Sternum 0.50



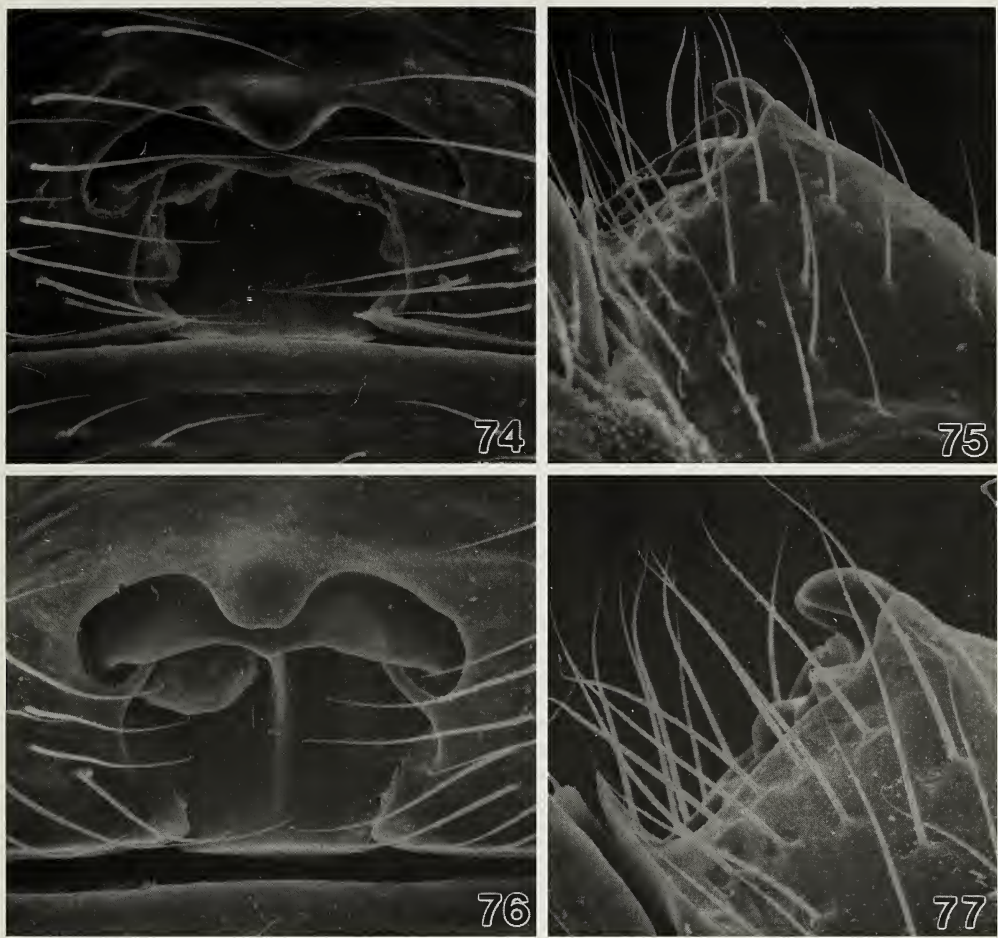
Figures 70–73.—*Alaranea merina* new species, male from Perinét, right palpus. 70. Retrolateral view; 71. Prolateral view; 72. Ventral view; 73. Parembolic process. PC = paracymbium; RMP = retromedian cymbial process.

long and wide; labium 0.12 long, 0.15 wide; palpal coxae 0.18 long, 0.14 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $2.44 + 0.44 + 1.96 + 1.84 + 1.08 = [7.76]$ ; II:  $2.12 + 0.44 + 1.72 + 1.72 + 0.96 = [6.96]$ ; III:  $1.30 + 0.38 + 1.00 + 0.96 + 0.64 = [4.28]$ ; IV:  $2.00 + 0.40 + 1.48 + 1.40 + 0.72 = [6.00]$ ; Palp:  $0.32 + 0.14 + 0.10 + (\text{absent}) + 0.26 = [0.82]$ . Palp (Figs. 70–73) with bulb marked as in *Alaranea betsileo* new species (Figs. 53, 54), cymbial RMP simple, pointed, PC slender in lateral view; tegulum apex strongly pustu-

late, TL large, projecting ventrally to form blunt point, denticulate over large area; C small, single; PP with apical recurved hook.

*Variation:* ( $n = 3$ ). Total length 2.29–2.71; ratios of carapace length/width 1.53–1.67, height/width 0.34–0.47; ratios of PER/OQP 2.18–2.44, PER/OAL 2.00–2.09, OQP/OQA 0.82–1.00, distance PM-PL/diameter PM 1.00–1.67, diameter AM/PM 1.25–1.67; ratios of clypeal height/AM diameter 1.36–1.60, cheliceral length/clypeal height 2.55–3.28; ratio of sternum length/width 1.03–1.11; ratio of length femur I/carapace width 1.89–2.12. Car-





Figures 74–77.—Epigyna of *Alaranea* spp. 74, 76. Ventral view; 75, 77. Lateral view; 74, 75. *Alaranea betsileo* new species, Talatakely; 76–77. *Alaranea merina* new species, Perinét.

apace with or without faint dusky radii extending from thoracic fovea; abdominal dorsum (Figs. 65, 66) clear with dorsolateral markings visible to obscured to varying degrees by black, these markings range from median transverse band or U to large dark area, lateral black marks present or absent.

*Female* (7 km. W Ranomafana): Total length 2.28. Markings as in male except abdomen having dorsomedian brown bands fainter, lateral black spots larger, and posterior spot smaller. Carapace 0.92 long, 0.58 wide, 0.24 high; PER 0.33 wide, AER 0.36 wide, OAL 0.18; ratio of eyes AM:AL:PM:PL: 1.6: 1.2:1.0:1.2, PM diameter 0.06. Clypeus 0.11 high, chelicerae 0.28 long. Sternum 0.46 long, 0.48 wide; labium 0.11 long, 0.14 wide; palpal coxae 0.17 long, 0.12 wide. Leg measurements (femur + patella + tibia + metatarsus

+ tarsus = [Total]): I: 2.24 + 0.44 + 1.80 + 1.72 + 1.06 = [7.26]; II: 2.00 + 0.42 + 1.60 + 1.48 + 1.02 = [6.52]; III: 1.24 + 0.36 + 0.92 + 0.84 + 0.76 = [4.12]; IV: 1.84 + 0.40 + 1.36 + 1.20 + 0.78 = [5.58]; Palp: 0.21 + 0.09 + 0.11 + (absent) + 0.22 = [0.63]. Epigynum and vulva as in *Alaranea betsileo* new species, epigynum as in Figs. 76, 77; vulva as in Fig. 91.

*Variation:* ( $n = 4$ ). Total length 2.00–2.82; ratios of carapace length/width 1.55–1.60, height/width 0.31–0.39; ratios of PER/OQP 2.09–2.55, PER/OAL 1.83–2.44, OQP/OQA 0.86–1.00, distance PM-PL/diameter PM 0.88–1.50, diameter AM/PM 1.25–1.67; ratios of clypeal height/AM diameter 1.10–1.50, cheliceral length/clypeal height 2.83–3.67; ratio of sternum length/width 1.03–1.15; ratio of length femur I/carapace width 1.87–2.17. Car-

apace yellow-brown to orange-brown, may be darker along margins of pars cephalica; abdominal dorsum with faint longitudinal brown bands exposed (Fig. 65) or obscured by small to large dorsolateral black spot (Fig. 66), may have posterior lateral dark spot or wavy line.

**Natural history.**—Common inside forest hanging beneath sheet webs between 0.2–2 m above ground.

**Distribution.**—Widespread in mid-elevation forests along the eastern side of the escarpment (Fig. 98).

**Material examined.**—**MADAGASCAR:** *Fianarantsoa Province:* 43 km. S Ambalavao, Reserve Andringitra, 22°14'S, 47°00'E, elev. 825 m, sifted litter, rainforest, 1♂, 5 October 1993 (B. L. Fisher) (CAS); Massif Andringitra, Mahaso, elev. 2100 m, 1♀, October 1971 (B. Ranson) (MRAC); Parc National de Ranomafana: around research cabin, 2♂3♀, 26 March 1992 (V. & B. Roth, S. Kariko) (MCZ). Parc National de Ranomafana, from foliage, ca. 21°12'S, 47°27'E, elev. ca. 1000 m, 1♂3♀, April 1992 (V. & B. Roth, S. Kariko) (CAS); 7 km. W Ranomafana, elev. 1100 m, 1♀, 22–31 October 1988, 2♂3♀, 1–7 November 1988 (W.E. Steiner) (USNM); Elev. 1200 m, 1♀, 22 October 1988 (W. Steiner, C. Kremen, R. Van Epps) (USNM); Parc National de Ranomafana, Vohiparara, ca. 21°14'S, 47°24'E, elev. 1100 m, 4♀, 5–7 November 1993 (N. Scharff, S. Larcher, C. Griswold, R. Andriamasamanana) (CAS, USNM, ZMUC). Parc National de Ranomafana, Talatakeley, 21°15'S, 47°25'E, elev. 900 m, 7♂21♀, 5–7 December 1993 (C. Griswold, N. Scharff, S. Larcher, and R. Andriamasamanana) (CAS, USNM, ZMUC). *Toamasina Province:* Parc National Perinét, near Andasibe, 18°56'S, 48°24'E, elev. 1000 m, montane rain forest, 40♂30♀, 4–5 November 1993 (J. Coddington, S. Larcher, C. Griswold, R. Andriamasamanana, & N. Scharff) (CAS, USNM, ZMUC); Perinét, 18°55'S, 48°25'E, 1♀, 1–3 August 1992 (V. & B. Roth) (CAS); Forêt de Didy, arbustes, 1♂, March 1947 (MNHN); Mandraka, batage, 3♂7♀, December 1946 (J. Millot) (MNHN); Beanana, 15°44'S, 49°28'E, 1♂, February 1970 (A. Lambillon) (MRAC).

#### *Alaranea alba* new species

Figs. 55, 57, 58, 67–69, 78–83, 92, 98

**Types.**—Male holotype and 1♂3♀ paratypes from Beria, Madagascar, June 1969 (A. Lambillon) (MRAC 142.978), MRAC except 1♂1♀ (CAS).

**Etymology.**—The species name refers to the largely white coloration.

**Diagnosis.**—Conductor undivided, proximal point elongate attenuate (Figs. 58, 79,

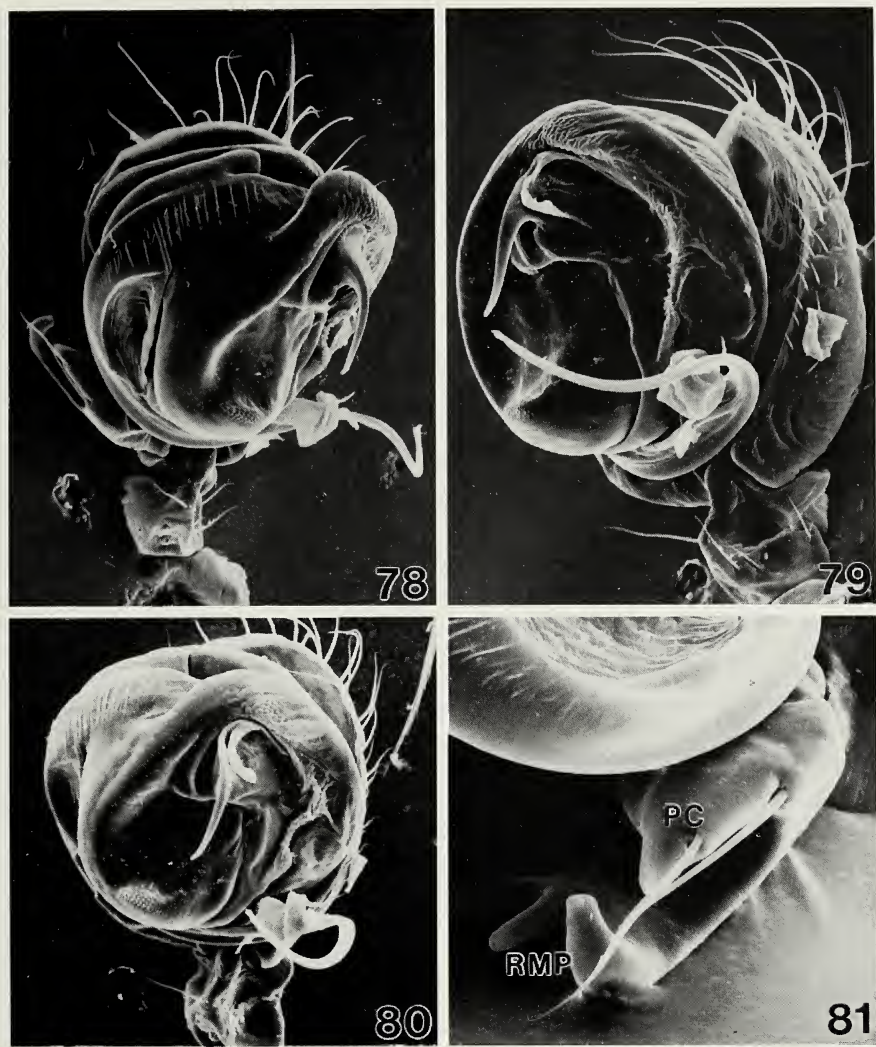
80); sternum pale yellow-brown, abdomen white marked only with lateral, ventral, and posterior black spots (Figs. 67–69).

**Description.**—*Male (holotype):* As in Figs. 67–69. Total length 1.80. Carapace pale yellow-brown, unmarked, thoracic fovea brown, ocular area black on ocular quadrangle and between lateral eyes; clypeus, chelicerae, sternum, labium, and palpal coxae yellow-brown, unmarked; legs and palpi yellow-white, unmarked; cymbium and tegulum yellow-brown; abdomen white, with brown sclerotization extending from epigastric furrow to and surrounding pedicel to form annulate petiole, dorsum with faint dorsolateral dusky markings beneath shiny transparent scutum, with black oval spots laterally, ventrally, and at posterior apex. Carapace 0.86 long, 0.58 wide, 0.30 high, oval in dorsal view; PER 0.35 wide, AER 0.34, OAL 0.16; ratio AM:AL:PM:PL, 1.2:1.0:1.0:1.5, PM diameter 0.05. Clypeus 0.10 high, chelicerae 0.32 long. Sternum 0.44 long, 0.42 wide; labium 0.08 long, 0.12 wide; palpal coxae 0.16 long, 0.10 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $1.92 + 0.36 + 1.48 + 1.44 + 0.96 = [6.16]$ ; II:  $1.72 + 0.36 + 1.44 + 1.36 + 0.88 = [5.76]$ ; III:  $1.12 + 0.28 + 0.72 + 0.88 + 0.56 = [3.56]$ ; IV:  $1.60 + 0.30 + 1.20 + 1.04 + 0.64 = [4.78]$ ; Palp:  $0.28 + 0.10 + 0.08 + (\text{absent}) + 0.28 = [0.74]$ . Palp (Figs. 57, 58, 78–81) with cymbial RMP bifid, with outer ventrad- and inner distad-directed processes, PC slender, pointed in lateral view; tegulum apex weakly pustulate, TL pointed ventrally, denticulate area small; C large, single, complex, with prolateral smooth concavity and retrolateral slender basad-directed process; PP large, swollen, with recurved apical process.

**Variation:** ( $n = 2$ ). Total length 1.80–1.84; ratio of carapace height/width 0.40–0.52; ratios of PER/OQP 2.54–2.69, PER/OAL 2.19–2.36, OQP/OQA 0.93–1.00, distance PM-PL/diameter PM 1.40–1.50, diameter AM/PM 1.20–1.50; ratios of clypeal height/AM diameter 1.67–2.33, cheliceral length/clypeal height 1.93–3.20; ratio of sternum length/width 0.91–1.04; ratio of length femur I/carapace width 1.63–1.65.

**Female (paratype):** Total length 1.72. Markings and structure as in male, except sclerotization of abdominal petiole weaker, yellow-white. Carapace 0.82 long, 0.54 wide,





Figures 78–81.—*Alaranea alba* new species, holotype male, right palpus. 78. Retroventral view; 79. Proventral view; 80. Ventral view; 81. Cymbial base, retroapical view. PC = paracymbium; RMP = retromedian cymbial process.

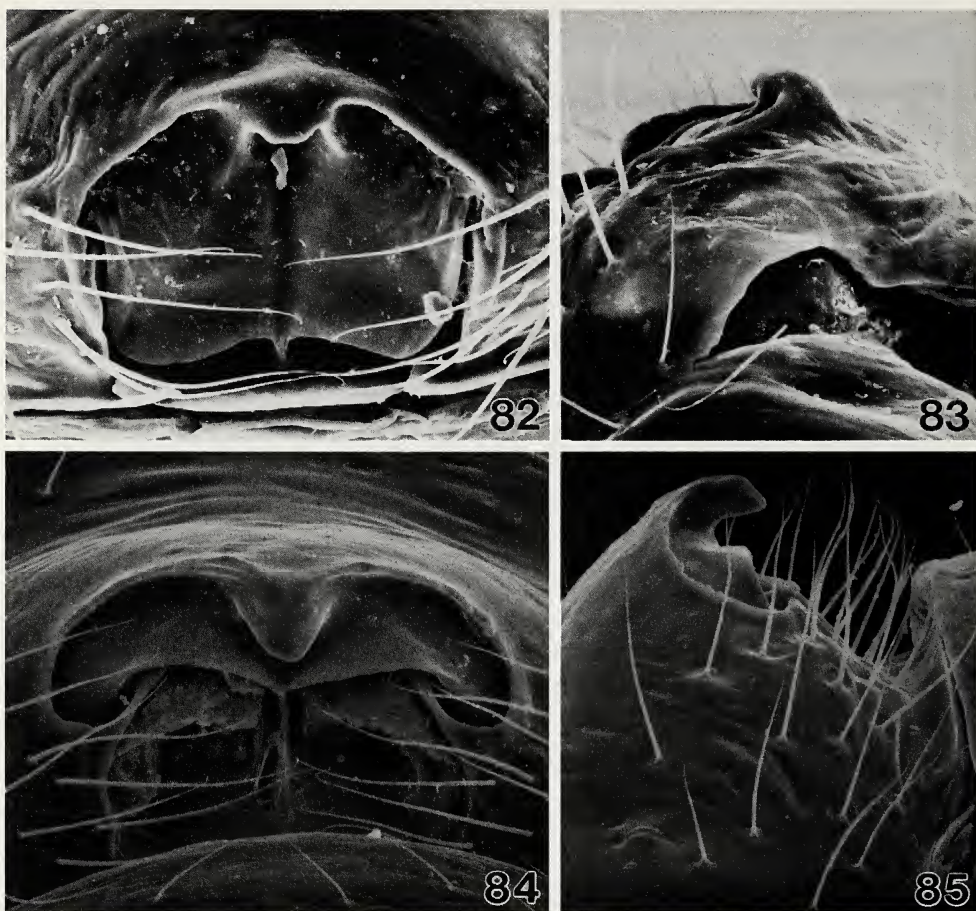
0.26 high; PER 0.30 wide, AER 0.29 wide, OAL 0.12; ratio AM:AL:PM:PL, 1.5:1.0:1.0:1.0, PM diameter 0.05. Clypeus 0.10 high, chelicerae 0.24 long. Sternum 0.40 long and wide; labium 0.08 long, 0.12 wide; palpal coxae 0.12 long, 0.10 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I: 2.08 + 0.36 + 1.76 + 1.68 + 1.12 = [7.00]; II: 2.00 + 0.36 + 1.64 + 1.52 + 0.96 = [6.48]; III: 1.16 + 0.28 + 0.72 + 0.84 + 0.60 = [3.60]; IV: 1.80 + 0.32 + 1.40 + 1.20 + 0.80 = [5.52]; Palp: 0.20 + 0.08 + 0.12 + (absent) + 0.20 = [0.60]. Epigynum as in Figs. 55, 82, 83, distance from tip of S to posterior margin greater than in

*Alaranea betsileo* new species; vulva as in Fig. 92, hemispherical AD relatively larger in relation to HS than in other *Alaranea*.

*Variation:* ( $n = 3$ ). Total length 1.64–1.84; ratios of carapace/width length 1.39–1.52, height/width 0.38–0.48; ratios of PER/OQP 2.14–2.50, PER/OAL 2.50–2.58, OQP/OQA 0.86–1.00, diameter AM/PM 1.00–1.20; ratios of clypeal height/AM diameter 1.67–2.40, cheliceral length/clypeal height 2.50–2.60; ratio of sternum length/width 0.95–1.05; ratio of length femur I/carapace width 1.78–1.92.

**Distribution.**—Known only from the type locality near Beria at 19°40'S, 45°23'E, in To-liara Province, Madagascar (Fig. 98).





Figures 82–85.—Epigyna of *Alaranea* spp. 82, 84. Ventral view; 83, 85. Lateral view; 82, 83. *Alaranea alba* new species, paratype; 84, 85. *Alaranea ardua* new species, Marojejy.

**Material examined.**—Only the type series.

*Alaranea ardua* new species

Figs. 84–89, 93–98

**Types.**—Male holotype and female paratype from Madagascar, Antsiranana Province, Marojejy Reserve, 8.4 km NNW Manantenina, montane rain forest, 14°26'S, 49°45'E, elev. 700 m, 10–16 November 1993, C. Griswold (CAS).

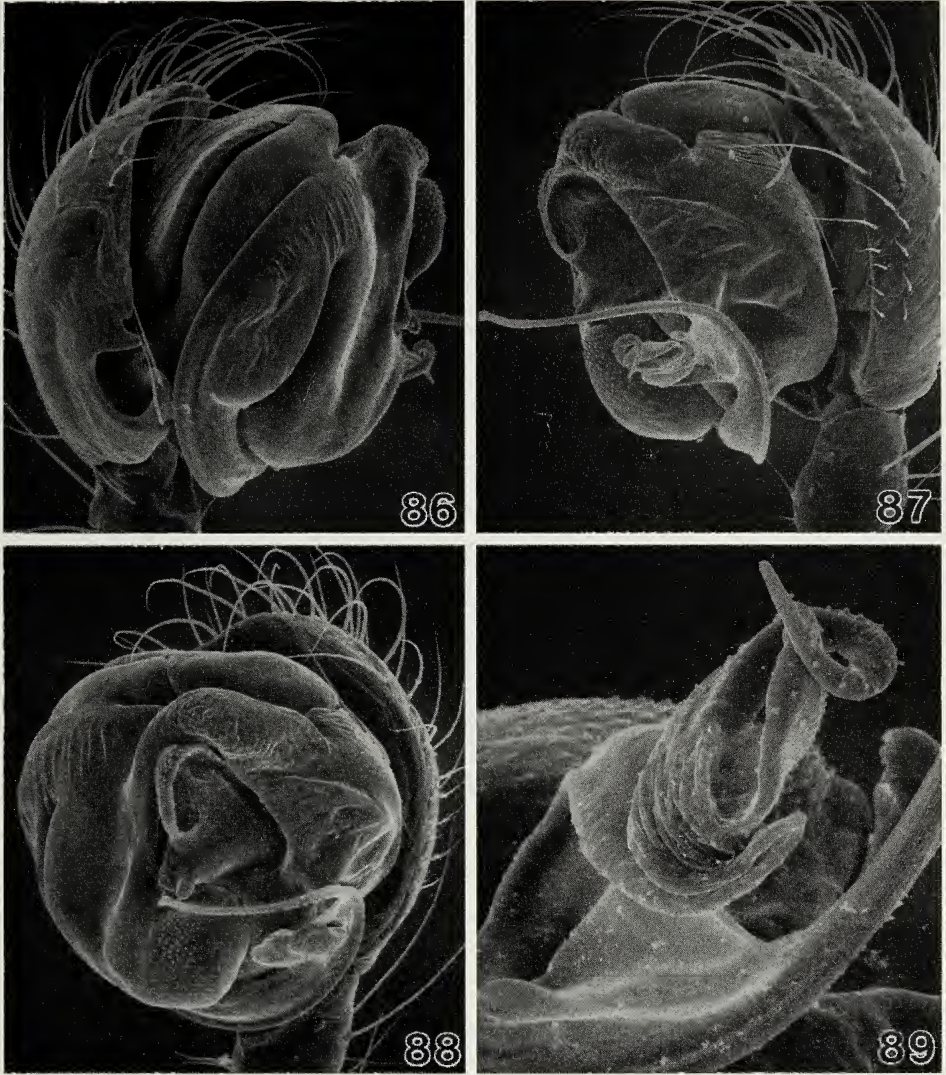
**Etymology.**—The species name is from the Latin for difficult, hard-won.

**Diagnosis.**—Conductor simple, proximal point thick, bifid, equal in width to cup (Figs. 86–88); dorsum of abdomen with sinuate longitudinal dark bands diverging from apex to middle and converging posteriorly (Figs. 95, 96). There seem to be no consistent characters to separate females of *ardua* from *merina*,

though the carapace of *ardua* (Fig. 96) tends to be darker than that of *merina* (Fig. 66).

**Description.**—*Male (holotype):* Total length 2.79. Carapace (Fig. 95) dusky orange-brown, faintly mottled with grey, especially along lateral margin, small dark longitudinal band anterior of thoracic fovea; ocular area black surrounding AM and lateral eyes, ocular quadrangle dark grey; clypeus yellow-brown, dark grey mark beneath AM narrowing to clypeal margin; chelicerae orange-brown, with faint dark basal streaks; sternum, labium, and palpal coxae red-brown with dark mottling, sternum black along ridges of rugosity, appearing nearly black; coxae, legs and palpi white, unmarked, palpal tibia yellow-brown, cymbium dark red-brown (Fig. 94); abdomen white, dorsum (Fig. 95) with paired longitudinal dark grey bands beneath transparent





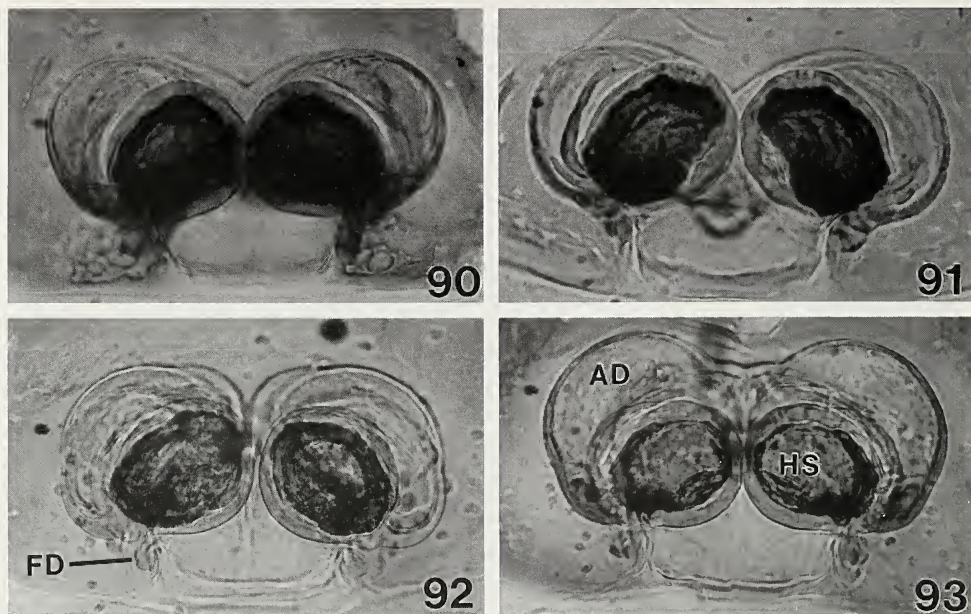
Figures 86–89.—*Alaranea ardua* new species, male from Marojejy, right palpus. 86. Retrolateral view; 87. Prolateral view; 88. Ventral view; 89. Parembolic process.

shiny scutum, area between these bands dusky, sides and posterior apex with black spots, venter grey between epigastric furrow and spiracle, dark brown sclerotization extending from epigastric furrow to and surrounding pedicel to form annulate petiole. Carapace 1.24 long, 0.76 wide, 0.35 high, trapezoidal in dorsal view; PER 0.47 wide, AER 0.44 wide, OAL 0.21; ratio AM:AL:PM:PL, 1.28:1.14:1.0:1.14, PM diameter 0.07. Clypeus 0.14 high, chelicerae 0.34 long. Sternum 0.59 long, 0.58 wide; labium 0.13 long, 0.18 wide; palpal coxae 0.21 long, 0.16 wide. Leg measurements (femur + patella + tibia +

metatarsus + tarsus = [Total]): I:  $1.53 + 0.28 + 1.28 + 1.13 + 0.70 = [4.92]$ ; II:  $1.51 + 0.25 + 1.17 + 1.04 + 0.64 = [4.61]$ ; III:  $0.98 + 0.23 + 0.64 + 0.59 + 0.38 = [2.82]$ ; IV:  $1.28 + 0.21 + 0.96 + 0.85 + 0.45 = [3.75]$ ; Palp:  $0.18 + 0.07 + 0.05 + (\text{absent}) + 0.18 = [0.48]$ . Palp (Figs. 86–89) with bulb marked as in *Alaranea betsileo* new species, cymbial RMP very short, acute, PC slender in lateral view; tegulum apex pustulate, TL large, convex, denticulation extensive; C large, retrolaterally dentate, with projecting basal article; PP with apical recurved hook.

*Variation:* ( $n = 3$ ). Total length 2.57–3.00;





Figures 90–93.—Vulvae of *Alaranea* spp., cleared, dorsal view. 90. *Alaranea betsileo* new species, from 7 km W Ranomafana; 91. *Alaranea merina* new species, Mandraka; 92. *Alaranea alba* new species, paratype; 93. *Alaranea ardua* new species, Marojejy. AD = afferent duct; FD = fertilization duct; HS = spermathecal head.

ratios of carapace length/width 1.60–1.64, height/width 0.45–0.46; ratios of PER/OQP 2.25–2.55, PER/OAL 2.00–2.25, OQP/OQA 0.81–1.11, distance PM-PL/diameter PM 1.00–1.43, diameter AM/PM 1.14–1.57; ratios of clypeal height/AM diameter 1.44–1.62, cheliceral length/clypeal height 2.19–3.30; ratio of sternum length/width 1.02–1.07; ratio of length femur I/carapace width 1.90–2.15. Markings of carapace range from dusky orange-brown to dark brown, dorsum of abdomen with longitudinal dark markings narrow and separate (Fig. 95) to completely black beneath scutum, lateral transverse marks forming spot or band connected to dorsum.

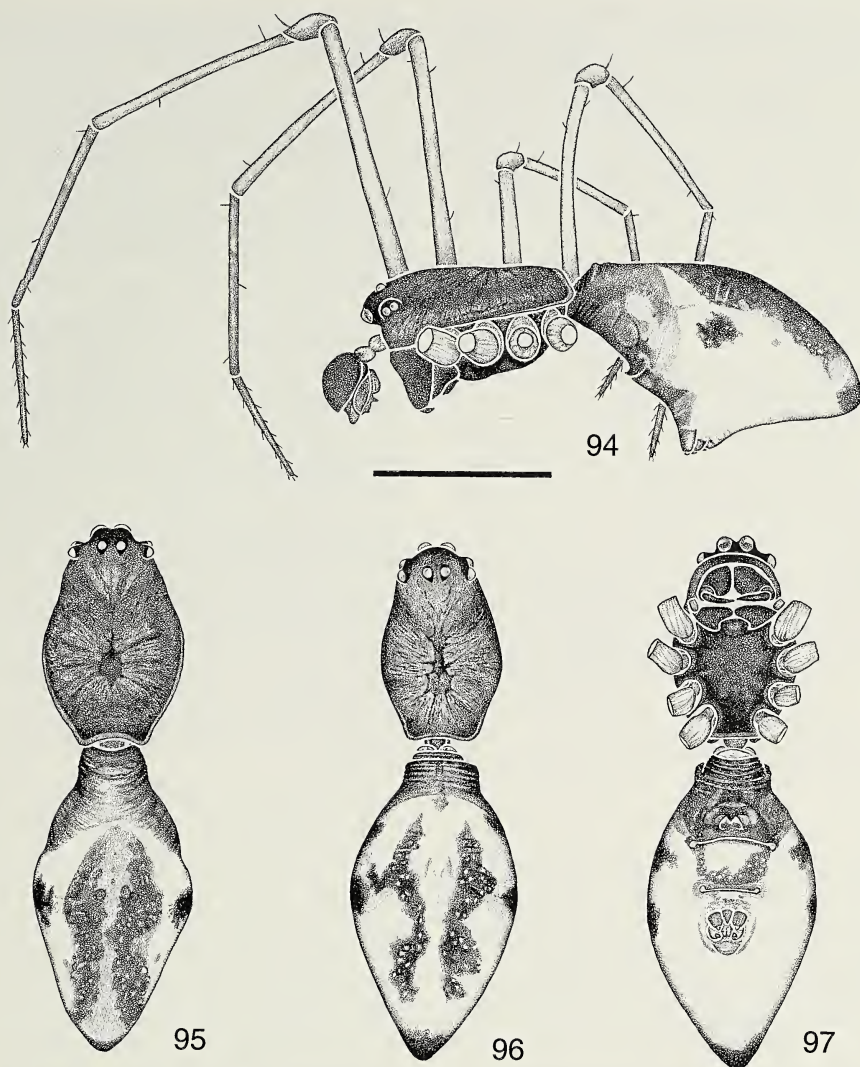
*Female (paratype)*: Total length 2.74. Markings (Figs. 96, 97) as in male except chelicerae, abdomen, and palpal coxae dark red-brown, sternum and petiole black, dorsum of abdomen with broad median black mark, this extending anteriorly to sclerotized petiole in two bands surrounding white mark, and extending laterally to form median transverse band, posterior tip black, venter pale. Carapace 1.13 long, 0.71 wide, 0.31 high; PER 0.45 wide, AER 0.43 wide, OAL 0.20; ratio AM:AL:PM:PL, 1.5:1.33:1.0:1.17, PM diameter 0.06. Clypeus 0.11 high, chelicerae 0.35

long. Sternum 0.56 long, 0.48 wide; labium 0.11 long, 0.19 wide; palpal coxae 0.21 long, 0.13 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I: 1.34 + 0.28 + 1.15 + 1.23 + 0.64 = [4.64]; II: 1.28 + 0.25 + 1.21 + 1.15 + 0.64 = [4.53]; III: 0.76 + 0.21 + 0.55 + 0.51 + 0.40 = [2.43]; IV: 1.17 + 0.21 + 0.87 + 0.74 + 0.47 = [3.46]; Palp: 0.26 + 0.08 + 0.14 + (absent) + 0.26 = [0.74]. Epigynum and vulva as in *Alaranea betsileo* new species, epigynum as in Figs. 84, 85; vulva as in Fig. 93.

*Variation*: ( $n = 3$ ). Total length 2.32–3.46; ratio of carapace height/width 0.45–0.52; ratios of PER/OQP 2.16–2.39, PER/OAL 2.16–2.26, OQP/OQA 0.90–1.00, distance PM-PL/diameter PM 1.00–1.43, diameter AM/PM 1.28–1.50; ratios of clypeal height/AM diameter 1.11–1.40, cheliceral length/clypeal height 3.00–3.80; ratio of sternum length/width 1.02–1.15; ratio of length femur I/carapace width 1.98–2.20. Markings of carapace range from orange except black ocular area to all dark brown; dorsal abdominal markings range from faint to bold, dorsolateral bands may be narrow and broken, solid and separate (Fig. 96) or meeting medially, or entirely black.

*Natural History*.—Common inside forest





Figures 94-97.—Morphology of *Alaranea ardua* new species, from Marojejy. 94, 95. Male; 96, 97. Female; 94. Lateral view; 95, 96. Dorsal view; 97. Ventral view. (Scale bar = 1 mm)

hanging beneath sheet webs between 0.2–2 m above ground.

**Distribution.**—Known only from the type locality (Fig. 98).

**Material examined.**—**MADAGASCAR:** *Antsi-ranana Province*, Marojejy Reserve, 8.4 km NNW Manantenina, montane rain forest, 14°26'S, 49°45'E, elev. 700 m, 10–16 November 1993 (J. Coddington, N. Scharff, S. Larcher, C. Griswold, and R. Andriamasamanana) 13♂11♀ (CAS, ZMUC, USNM).

#### DISCUSSION

So far as is known, Malagasy cyatholipids occur in moist forest, the majority being re-

corded from above 600 m elevation along the eastern slopes of the central mountain chain (Fig. 98). At least *Alaranea merina* new species occurs at over 2000 m. *Ulwembua antsi-ranana* new species, which occurs in an area of local orographic rainfall, is disjunct from the main distribution of Cyatholipidae. Restriction to moist forest appears likely. Collecting by the author and colleagues in drier habitats never revealed Cyatholipidae.

At least two Malagasy genera, *Ulwembua* and *Alaranea*, show affinities to taxa occurring in tropical or subtropical montane forests of eastern Africa. *Ulwembua* was previously known from three species from South Africa

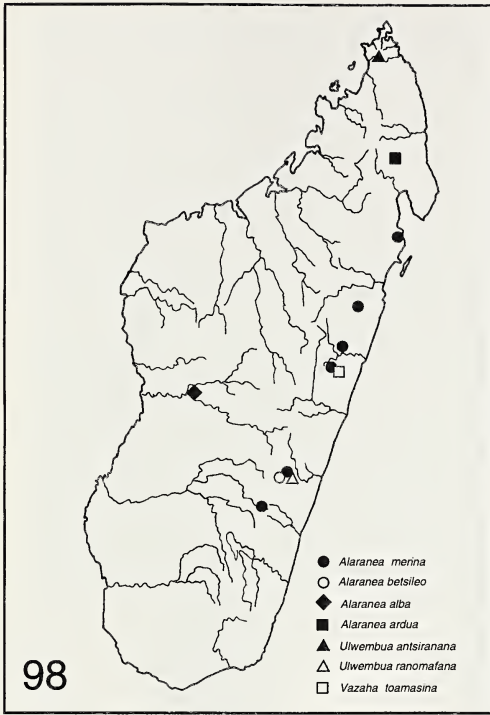


Figure 98.—Map showing distributions of Cyatholipidae in Madagascar.

(Griswold 1987): *U. outeniqua* Griswold from the coastal forests of central Cape Province, and *U. pulchra* Griswold and *U. denticulata* Griswold from Zululand. Undescribed species of *Ulwembua* also occur in the mountains of Tanzania. *Alaranea* new genus shows affinities to an undescribed genus occurring in montane forests from Malawi to Kenya. The distribution of the sister groups of these Malagasy cyatholipids is consistent with the Afromontane biogeographic pattern detailed for spiders by Griswold (1991) in which the sister area of Madagascar comprises the tropical montane forests of the eastern part of Africa. Several groups of spiders, including *Phyxelida* and the *Lamaika* group of the Amaurobiidae Phyxelidinae (Griswold 1990) and *Ulwembua* and *Alaranea* of the Cyatholipidae, show this intercontinental disjunction, suggesting that their distribution is not the result of accidental dispersal. Their distribution may date from times of former connection or at least greater proximity between Madagascar and eastern Africa, perhaps in the Mesozoic (Rabinowitz et al. 1983). Phylogenetic and biogeographic evidence continues to support the suggestion

that the Afromontane biota, at least the arachnid component, is ancient.

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## A NEW SPECIES OF *SCHIZOCOSA* FROM THE SOUTHEASTERN USA (ARANEAE, LYCOSIDAE)

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**ABSTRACT.** A new species of *Schizocosa* (Araneae, Lycosidae) is described and illustrated. *Schizocosa uetzi* new species is locally abundant in the southeastern USA and is mature during June and July. Morphological characters, coloration and courtship behavior separating this new species from its closely related congeners are noted.

Members of the wolf spider genus *Schizocosa* Chamberlin 1904 from the Nearctic Region were last revised by Dondale & Redner (1978). Since that time, two additional species have been described from the region by Uetz & Dondale (1979) and Stratton (1991). Within the genus there are at least two species groups that appear to be diverging by secondary sexual characteristics and by courtship behavior. The group best studied so far is the *Schizocosa ocreata* species group, defined by the presence of a finger-like paleal process on the male's palp and by paired excavations on the transverse piece of the female's epigynum. The group includes *S. ocreata* (Hentz 1844), *S. crassipes* (Walckenaer 1837), *S. floridana* Bryant 1934, *S. rovneri* Uetz & Dondale 1979, *S. stridulans* Stratton 1991 and *S. uetzi* new species. Uetz & Dondale (1979) described *S. rovneri* as the sister group to *S. ocreata*, the two differing only in the presence (in *ocreata*) or absence of the distinctive tibial bristles found on the first pair of legs; they are otherwise identical. Uetz & Denterlein (1979) described the courtship behavior of *S. rovneri* and demonstrated that courtship behavior serves as an isolating mechanism between *S. ocreata* and *S. rovneri*. This species and *S. stridulans* were first recognized as new species by differences in male secondary sexual characteristics (lack of pigment on tibia of males of *S. rovneri*, pigment but not bristles found on the tibia and distal portion of the femora in males of *S. stridulans*); and later, the courtship behavior in each was found to be distinct and to function as an isolating mechanism (Uetz & Denterlein 1979; Stratton

1991; in press). *Schizocosa uetzi* new species was first noted from collections from the southeastern USA made by W.P. Maddison in 1984 and by the author and L. Williams in 1985. In each case, specimens were collected that keyed to *S. ocreata*, but secondary sexual characteristics did not match any of the known species. Subsequent work demonstrated that this species has a consistent pattern of secondary sexual characteristics and distinctive courtship behaviors.

### METHODS

Wolf spiders were collected throughout the southeastern USA during the springs and summers of 1991-1995. Immature and mature individuals were returned to the laboratory at the University of Mississippi where they were individually maintained in vials (8.5 cm × 5 cm) with wicks that extended into a water tray providing a constant source of moisture. Immature spiders were held until they matured, and mature spiders were held for behavioral studies. Appropriately-sized crickets were offered twice weekly as food for the spiders. Temperature in the laboratory ranged from 22-25 °C. Temperature during courtship and copulatory studies was 22-25 °C. Spiders were exposed to an L:D schedule of 14:10 h. Animals for behavioral studies were observed from within a few days to a few weeks of collection.

Courtship and copulation were observed by setting the female in a culture dish with a piece of filter paper 6-12 h before observations. Males and females were then placed in an observation chamber with the filter paper



where their interactions were videotaped using a Panasonic HD-5000 videocamera with a 105 mm macrolens. Sounds were recorded from the substrate by a stereo-needle transducer attached to an EG&G PARC, Model 113, preamp (Gain set at 5K, low roll off set at 0.3 Hz, high roll off at 10 kHz) and were overlaid onto videotape. Both courtship behaviors and copulatory behaviors were videorecorded.

Measurements were made of mature specimens (males,  $n = 22$ ; females,  $n = 8$ ) with an ocular micrometer. Terminology is as used in Dondale & Redner (1978) and Stratton (1991). The following abbreviations are used for collectors and for museum depositions: GES = Gail E. Stratton, PRM = Patricia R. Miller, GLM = Gary L. Miller, WRM = William Miller, GTB = Gerry Baker, EAH = Eileen Hebets, WG = Wendy Garrison, KW = Kimball White, LLW = Lisa Williams, WPM = Wayne Maddison, TS = Terry Schiefer, ME = Micky Eubanks, KB = Kari Benson. Museums: National Museum of Natural History Smithsonian Institution (USNM); American Museum of Natural History (AMNH); California Academy of Science (CAS); Mississippi Entomological Museum (MEM); Museum of Comparative Zoology (MCZ); Florida State Collection of Arthropods (FSCA); Biosystematics Research Institute, Canada (BRI); Field Museum of Natural History (FMNH). Specimens in the collection of the author are held at the University of Mississippi (UM).

*Schizocosa uetzi* new species

Figs. 1–6

**Holotype.**—Male from USA, Mississippi, Lafayette County, 8 mi SE Oxford, T10S R3W Sec. 35; 34°36'N, 89°29'W; 10 June 1991 (G. Stratton, P.R. Miller, G.L. Miller, W.R. Miller, M. Eubanks). Illustrated specimen. Collection #91–14; night, mixed pine, hardwood. Deposited in USNM.

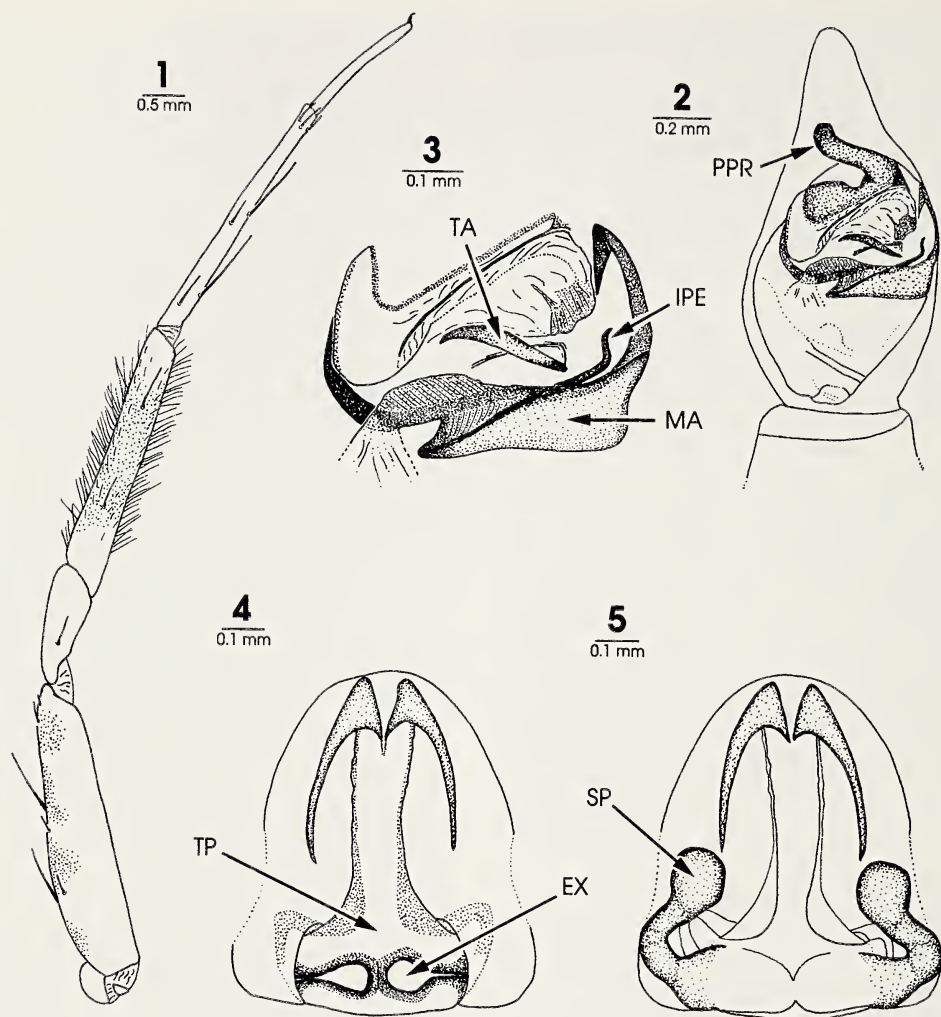
**Paratypes.**—**MISSISSIPPI:** *Lafayette County*, 8 mi SE Oxford, “Lonesome 80”, T10S R3W Sec. 35; 34°36'N, 89°29'W; mixed pine hardwood, 1♀, 10 June 1991 (G. Stratton, P.R. Miller, G.L. Miller, W.R. Miller, M. Eubanks), night, mixed pine hardwood (USNM); 2♂ (MEM); 2♂ (AMNH); 2♂ (FMNH); 2♂ (MCZ); 2♂ (CAS); 2♂ (BRI); 2♂ (FSCA). 28 June–5 July 1993, 2♂ (USNM). **LOUISIANA:** *Natchitoches Parish*,

Kisatchie National Forest, “Red Dirt Area,” 10♂, coll. 23 May 1993, matured 7–25 June (GES, PRM) (UM), 8♀, matured 6 June–27 June (UM).

**Etymology.**—The specific epithet is to honor Dr. George W. Uetz, spider ecologist, educator, mentor and friend.

**Diagnosis.**—Males of *Schizocosa uetzi* new species possess a finger-like process on the palea of the palp as all other members of the *ocreata* group (Fig. 1; see also Dondale & Redner 1978, figs. 1–3; Stratton 1991, figs. 1–4). *S. uetzi* can be distinguished from *ocreata* and *crassipes* by absence of a dense tibial brush, from *rovneri* by having patella and tibia I darker than the femur, and from *stridulans* in lacking a dark line on femur I and pigment on distal end of femur. *Schizocosa uetzi* is slightly, but significantly, larger than *S. stridulans* in total length, carapace length and carapace width ( $P < 0.5$ ;  $t$ -test) (Table 1) and although it is not significantly different in size from *S. rovneri* (Table 1), *S. uetzi* has longer legs relative to its body size than *S. rovneri* ( $P < 0.5$ ;  $t$ -test) (Table 2). Table 3 summarizes the differences in genitalic dimensions between these species. *Schizocosa uetzi* would probably not be confused with *S. floridana*, another member of this species group, as *S. floridana* is limited to Florida and has an undulating median band on the carapace that is different from all other members of this species group (Table 3). Females of *S. uetzi* new species can be confidently placed in the *ocreata* species group by the presence of paired excavations on the transverse piece of the epigynum. However, the specific determination can only be made when either *S. uetzi* new species is the only species in the *ocreata* group present in a habitat, or when a female is collected in *copula* with a male of *S. uetzi*. A key to adult males in the *S. ocreata* species group is provided.

**Description.**—**Males:** (Figs. 1–3) ( $n = 22$ ). For measurements see Table 1 (body length) and Table 2 (leg length). Cephalothorax brown; submarginal band narrow but distinct and wavy, sometimes with three spots on lateral sides; pale median band as wide as posterior lateral eyes with slight indentation at posterior one-third of the band. Sternum yellow-brown to light brown with no spots, always darker than coxae. Chelicerae brown, setaceous, with two dark stripes down anterior



Figures 1-5.—Leg I of male and genitalia of males and females of *Schizocosa uetzi* new species (male holotype; female paratype). 1. Leg I of mature male; 2. Ventral aspect of left palp; 3. Enlargement of palp; 4. External aspect of epigynum of female; 5. Internal aspect of epigynum of female. IPE = intramittent portion of embolus; MA = median apophysis; TA = terminal apophysis, PPR = paleal process; MS = median septum; TP = transverse piece; EX = excavation of transverse piece; SP = spermatheca.

side. Promargin of fang furrow with three unevenly-sized teeth; retromargin of fang furrow with three evenly-sized teeth. Femora I-IV yellow to light brown with 3-4 dark annulations. Patellae I-IV brown. Tibia I brown to dark brown with black hairs, always slightly but distinctly darker than tibiae II-IV, always darker than femora I (Fig. 1), sometimes with faint annulations. Tibiae II-IV yellow to light brown. Tibial length to width ratio larger for males than females (Table 2). Dorsum of abdomen in most specimens (16 of 21 specimens) with faint heart mark and with spots.

Venter of abdomen yellow with black spots. Population from Louisiana, Natchitoches Parish, with dark square of pigment near genital pore (6 of 6 specimens). Palpal cymbium with 7-13 terminal macrosetae. Palpal palea (PPR) with long distal process, sometimes slightly curved into an *s*-shape (Fig. 2). Median apophysis (MA) with distal margin convex. Intramittent part of embolus (IPE) slender, pointed with slight curve (Fig. 3). Terminal apophysis (TA) with thickened margin extending to base of IPE. Length of palp, cymbium and paleal process given in Table 3. File



Table 1.—Comparison of total length, cephalothorax length and cephalothorax width of *Schizocosa uetzi* new species, *S. rovneri* (measurements of males from collections of GES; females from Uetz & Dondale 1979) and *S. stridulans* (data from Stratton 1991). Measurements are in mm, means are  $\pm$  SD. Males are from type locality ( $n = 16$ ) and from LA, Natchitoches Parish ( $n = 6$ ); females from Natchitoches Parish ( $n = 8$ ). For any one characteristic measured, significant differences are indicated by different letters. Measurements that are followed by the same letter are not significantly different from each other (Students'  $t$ -test, two tailed,  $P < 0.05$ ).

	<i>Schizocosa uetzi</i>	<i>Schizocosa stridulans</i>	<i>Schizocosa rovneri</i>
Males			
Total length (mean)	7.16 $\pm$ 0.58 A	6.40 $\pm$ 0.43 B	6.78 $\pm$ 0.65 A
(range)	5.9–8.0	5.04–6.80	6.0–7.8
Cephalothorax length (mean)	3.59 $\pm$ 0.25 C	3.25 $\pm$ 0.33 D	3.6 $\pm$ 0.31 C
(range)	3.2–4.2	2.47–3.80	3.2–4.0
Cephalothorax width (mean)	2.75 $\pm$ 0.18 E	2.56 $\pm$ 0.24 F	2.75 $\pm$ 0.16 E
(range)	2.4–3.2	2.04–3.10	2.6–3.0
Sample size	22	51	9
Females			
Total length (mean)	9.5 $\pm$ 0.7 G	8.09 $\pm$ 1.21 H	7.3–10.4
(range)	8.6–10.6		
Cephalothorax length (mean)	4.0 $\pm$ 0.1 I	3.5 $\pm$ 0.4 J	4.0 $\pm$ 0.43
(range)	3.8–4.2		
Cephalothorax width (mean)	3.0 $\pm$ 0.2 K	2.68 $\pm$ 0.35 L	3.02 $\pm$ 0.31
(range)	2.6–3.2		
Sample size	8	61	7

of stridulatory organ at embolus base, scraper on distal tip of palpal tibia.

*Females:* (Figs. 4, 5) ( $n = 8$ ). Total length, cephalothorax length and width in Table 1. Females slightly larger than males. Cephalothorax brown, submarginal band narrow, distinct and wavy, pale median band as wide as posterior lateral eyes with slight indentation at posterior one third of band. Sternum brown to light brown with no spots, always darker than yellow coxae. Chelicerae brown, setaceous,

with two dark stripes down anterior side. Fang furrow as in male. Femora I-IV yellow and annulated, patellae and tibiae light brown with annulations sometimes present on tibiae. Leg segment lengths similar to male lengths (Table 2) except tibia and metatarsus shorter in female. Abdominal dorsum with heart mark, either distinct or faint (faint in 4 of 9 specimens), and chevrons. Abdominal venter yellow with black spots. Epigynum with excavations on transverse piece (Fig. 4); exca-

Table 2.—Comparison of length of segments of leg I in males ( $n = 21$ ) and females ( $n = 8$ ) of *Schizocosa uetzi* new species and males ( $n = 9$ ) of *Schizocosa rovneri*. Measurements are in mm and means are  $\pm$  SD.

	<i>Schizocosa uetzi</i> new species		<i>Schizocosa rovneri</i>
	Females	Males	Males
Femur	3.3 $\pm$ 0.2	3.56 $\pm$ 0.24	2.74 $\pm$ 0.96
Patella	1.6 $\pm$ 0.1	1.51 $\pm$ 0.12	1.36 $\pm$ 0.25
Tibia	2.7 $\pm$ 0.1	3.23 $\pm$ 0.23	2.63 $\pm$ 0.48
Metatarsus	2.6 $\pm$ 0.2	3.11 $\pm$ 0.75	2.59 $\pm$ 0.43
Tarsus	1.5 $\pm$ 0.1	1.66 $\pm$ 0.12	1.49 $\pm$ 0.26
Tibial width	0.5 $\pm$ 0	0.40 $\pm$ 0.1	0.40 $\pm$ 0.1
Ratio tibial length to width	5.4	8.1	6.6

Table 3.—Measurements of palps (*n* = 22) and epigyna (*n* = 8) of *Schizocosa uetzi* new species. Measurements are in mm and are given as means ± SD.

Male	
Palp length	1.22 ± 0.33
Cymbium length	0.77 ± 0.15
Cymbium width	0.61 ± 0.06
Paleal process	0.42 ± 0.06
Female	
Total epigynal length	0.8 ± 0
Depth of hood	0.1 ± 0
Width, transverse piece	
widest part	0.7 ± 0.1
Width, longitudinal piece	0.2 ± 0.1
Height of excavation	0.1 ± 0

variations (EX) usually triangular in shape, slightly asymmetrical, nearly meeting at midline. Longitudinal piece sometimes narrowing anteriorly (4 of 9 specimens) or sides parallel (as in Fig. 4; 5 of 9) or narrowing slightly at midline. Spermathecae (SP) ovoid and smooth (Fig. 5).

**Courtship behavior.**—The courtship behavior of this species involves distinctive movements on the part of both the males and the females. The following descriptions are based on videotaped courtships of five courting pairs from Lafayette County, Mississippi; and three pairs from Natchitoches Parish, Louisiana. Males show chemoexploratory behavior similar to that seen in other lycosids (Tietjen 1979) including *S. ocreata*, *S. rovneri*, (Uetz & Denterlein 1979) and *S. stridulans* (Stratton 1991), wherein the male ex-

Table 4.—Secondary sexual characteristics and courtship behavior, characteristics most useful in separating members of the *Schizocosa ocreata* species group that may be confused with *Schizocosa uetzi* new species (Dondale & Redner 1978; Uetz & Dondale 1979; Stratton 1991).

Species	Distinguishing features
<i>uetzi</i> new species	Secondary sexual characteristics: Males have some pigmentation on tibia and sparse hairs on tibia; tibia and patella I always slightly darker than femur I. Courtship behavior: Pulses of stridulation.
<i>rovneri</i>	Secondary sexual characteristics: Lacking, mature males lack bristles or conspicuous pigmentation on legs I. Tibiae I same color as femur of leg I. Courtship behavior: Body slams or “bounces” producing clear and distinct sounds (Uetz & Denterlein 1979).
<i>stridulans</i>	Secondary sexual characteristics: Males have black pigmentation on the tibia of legs I and halfway up the femur. Courtship behavior: Pulses of stridulation interspersed with tapping first pair of legs (Stratton 1991, in press).
<i>floridana</i>	Secondary sexual characteristics: Legs I of mature male are slightly darker than other legs. Courtship behavior: Pulses that begin with two abdominal dips (producing a “squeaking” sound), followed by two pulses of stridulation, followed by two taps with the front legs. Other characters: Pale submarginal band of cephalothorax broken into three semicircular patches that “break out” at carapace margins. Pale median band with undulating margins. Geographic distribution: limited to northern Florida and southern Georgia.
<i>crassipes</i>	Secondary sexual characteristics: Bristles on tibia of legs I black and dense. Courtship behavior: Behavior includes arch, extension and wave of legs I (Miller et al., in press).
<i>ocreata</i>	Secondary sexual characteristics: Bristles on tibia and metatarsus of legs I black and dense, bristles often extending to the basal portion of the tarsus. Courtship behavior: Active courtship involving extensive walking plus tapping and arching of legs I.



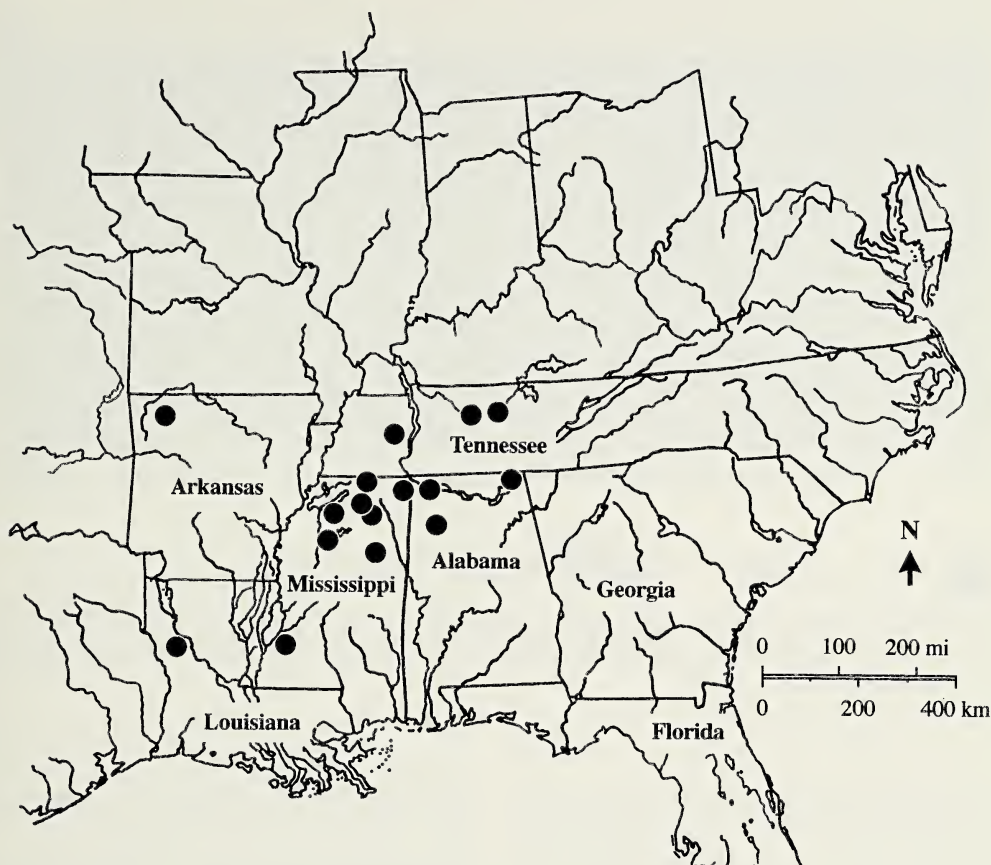


Figure 6.—Distribution of *Schizocosa uetzi* new species.

plores the substrate with the dorsal surface of his palp. Following chemoexploration, the male of *S. uetzi* new species typically performs several episodes of stridulation. In this behavior, the male assumes a stance with the body raised slightly from the substrate and stridulates by slight movements of the palps which are held nearly perpendicular to the substrate. The behavior is similar to that of *S. stridulans*, but there is no quick tapping of legs I as is seen with *S. stridulans* (Stratton 1991; Stratton in press).

Females show a distinctive abdomen dip that occurs in the midst of male courtship. There was no sound recorded with the movement, and it was seen only in animals that eventually mated.

Copulatory behaviors were very similar to the behaviors seen in *S. ocreata*, *S. crassipes*, *S. rovneri*, and *S. stridulans*. Males mounted so that the male's sternum was against the dorsal surface of the female's abdomen. The

male scraped his palp along the side of the female's abdomen; she rotated her abdomen and his palp engaged her epigynum. There was a single expansion of the hematodocha, the palp disengaged, and the male then re-engaged the palp with another expansion of the hematodocha. After many engagements, he switched sides and repeated the sequence on the other side (Stratton et al. 1996). The durations for four copulations were 90 min, 115 min, 115 min, and 130 min.

**Geographic distribution, phenology and habitat.**—*Schizocosa uetzi* new species has been collected from states throughout the mid-south region of the USA (Fig. 6). The species is the most common mid-sized wolf spider in June and July in northern Mississippi and northern Alabama; and it has been collected from Tennessee, western Arkansas and Louisiana. A single individual, collected from South Carolina, had a maturation time consistent with this new species. Except for this sin-

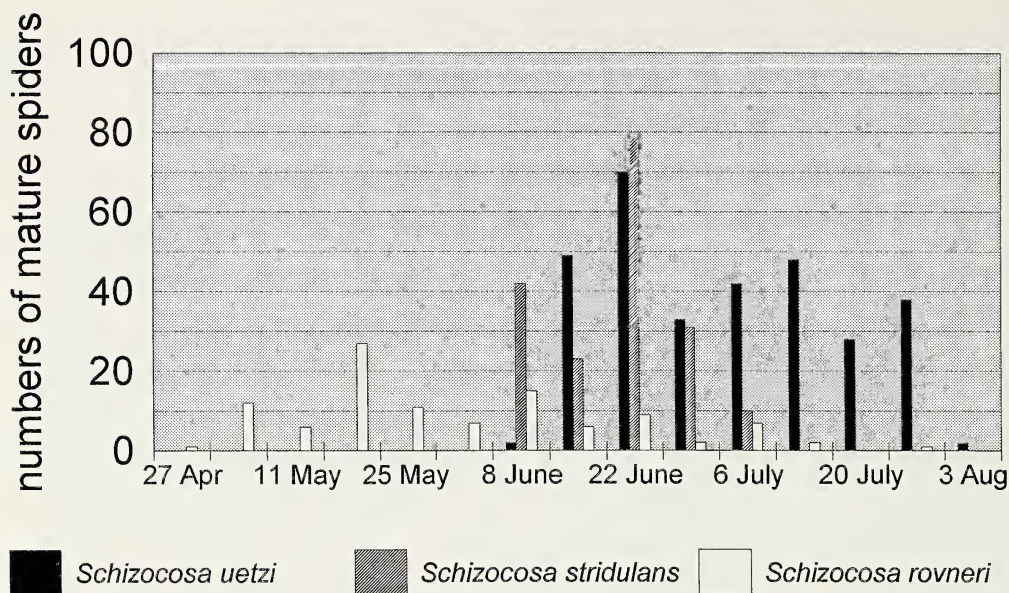


Figure 7.—Comparison of times of maturity of *Schizocosa uetzi* new species, *Schizocosa stridulans* and *Schizocosa rovneri* males in the southeastern USA, collections from 1991–1995. All individuals were caught by hand or pitfalls as adults.

gle male, all populations are from west of the Appalachian Mountains. Extensive wolf spider collections have not yielded specimens of *S. uetzi* new species from Florida.

Mature males have been collected from 7 June–2 August. There is broad overlap in phenology with *S. stridulans* (Fig. 7). Both *S. rovneri* and the brush-legged species *S. crassipes* occur much earlier in the season (Figs. 7, 8). In a year-long pitfall study in Grenada County, Mississippi, there was almost no overlap between *S. uetzi* new species and *S. crassipes* when the phenology of mature males was compared (Fig. 8).

In Mississippi, Tennessee, Arkansas and Louisiana, *S. uetzi* new species has consistently been found in upland deciduous leaf litter or upland deciduous litter mixed with pine litter. *Schizocosa uetzi* new species has frequently been collected with *S. stridulans* and shows broad geographic overlap with that species (Fig. 6, compare to fig. 14 in Stratton 1991) as well as overlap of habitat and phenology (Fig. 7). When *S. uetzi* new species and *S. stridulans* are collected together, *S. uetzi* is slightly but significantly larger (as seen in Mississippi, Lafayette County, “Bailey’s Woods”, 15 June 1993; Student’s *t*-test,  $t =$

5.91, 5.55, 6.48,  $P < 0.001$  for cephalothorax width, length and tibial length).

**Additional material.**—The following material was collected and identified as *Schizocosa uetzi* new species. **ALABAMA:** *Jackson County:* nr Russell Cave Natl. Monument, 1♂, day, 19 June 1992 (GES); *Lauderdale County:* Uplands of Tennessee River, West of Florence, 4♂, 18 June 1984, (GES, LLW); *Winston County:* W.B. Bankhead Natl. Forest at Natural Bridge, Winston County Rd. #63 N of Houston, deciduous woods nr. ravine, 8♂, night, 18 June 1992 (GES); Houston Campground, 2♂, night, 18 June 1992 (GES). **ARKANSAS:** *Logan County:* Mt. Magazine, Mossback Ridge, South Slope, 1♂, pitfall, 23 June 1990 (B. Leary); Mossback Ridge, North Slope, 3♂, pitfall, 20 July 1990 (B. Leary). **MISSISSIPPI:** *Claiborne County:* Rocky Springs Park, 1♂, coll. 17 May 1983, matured in June (WPM); uplands woods about 10 mi S. of Vicksburg, 2♂, coll. 20 May 1993, matured 14 June (GES, PRM). *Grenada County:* T21N R2E, Sec. 12, 13N, & R3E, Sec. 7S, 18N, 14♂, pitfall in deciduous woods, 5–11 June 1991 (PRM, GES, GTB); 3♂, day, 11 June 1991 (PRM, GES, TS, GTB); 15♂, 19–25 June (GTB); 21♂, 26 June–2 July 1991 (PRM, GTB); pitfall on sandbar of creek, 12♂, 26 June–2 July 1991 (PRM, GTB); deciduous woods, 5♂, night, 26 June 1991 (PRM, KB); pitfall deciduous woods, 10♂, 3–9 July 1991 (PRM); 2♂, 10–16



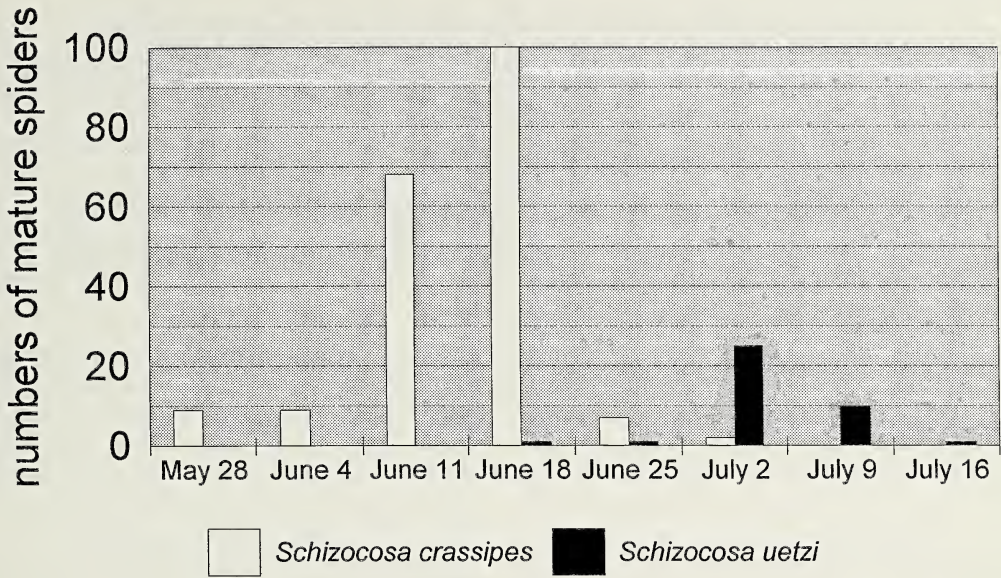


Figure 8.—Comparison of occurrence of mature males of *Schizocosa uetzi* new species and mature males of *Schizocosa crassipes* from a pitfall study in Grenada County, Mississippi in 1991.

July 1991 (PRM, GTB); 2♂, 17–23 July 1991 (PRM, GTB); 1♂, 26 July 1993 (GES, PRM, EAH, KW); 8♂, coll. 21 May 1994, matured in lab 10, 13, 23 June 1994 (GES, PRM); T22N R3E, Sec. 31NW, pitfall deciduous woods, 12♂, 19–25 June 1991 (PRM); 1♂, 10–16 July 1991 (GTB, PRM); deciduous woods by ravine, 1♂, 12 June 1991 (GES, PRM, TS, GTB). *Lafayette County*: Oxford, 1♂, 15 June 1984 (P.K. Lago); Old Taylor Rd., 2♂, 11 June 1991 (PRM, GES); 4♂, 2♀, night, 15 June 1991 (PRM, GES); deciduous woods, 3♂, night, 15 June 1993 (PRM, GES, EAH); Puskus Lake, 13 mi NE Oxford, 8♂, 11 June 1991 (PRM, WRM, GES); 3♂, 21 July 1993 (GES, PRM, EAH, KW); 2 mi NW Oxford, deciduous leaf litter, 1♂ 1♀, night, 30 June 1991 (PRM); Clear Creek Rec. Area, 2♂, night, 17 June 1992 (GES); Bailey's Woods, 12♂, night, 15 June 1993 (GES, PRM, GLM, EAH, WG, Young Scholars); 1♂, day, 15 June 1993 (EAH, KW); 10♂, night (EAH, GLM, WG); 8 mi SE Oxford, T10S R3W Sec.35; 34°36'N, 89°29'W, mixed pine and hardwood, "Lonesome 80," 19♂, night, 10 June 1991 (GES, PRM, GLM, WRM, ME); 1♂, coll. 25 May 1992 (GES), spider sacrificed, 18 June 1992 (GES); rocky exposed hillside, 1♂, night, 15 June 1992 (GES); 2♂, 1 July 1992 (PRM, GES); 1♂, night, 4 July 1992 (GES); 3♂, 4 July 1992 (GES); day on hill by small lake, 4♂, 23 June 1993 (GES, EAH, KW); 4♂, night, 1 July 1993 (GES, EAH, PRM); pitfalls from 26 May, 1992 to July 1993, 9♂, 3–10 June 1992 (GES, PRM); 5♂, 16–24 June 1992, 6♂, 24 June–1 July 1992, 17♂, 1–8 July 1992, 12♂, 8–15 July 1992, 14♂, 15–22 July

1992, 2♂, 22–29 July 1992, 4♂, 10–20 June 1993, 2♂, 20–28 June 1993, 14♂, 28 June–5 July 1993, 12♂, 5–12 July 1993, 14♂, 12–21 July 1993 (GES, PRM). *Marshall County*: Wall Doxey State Park, T5S R3W Sect. 12, 89°24'W, 34°40'N, edge of deciduous woods, 1♂, coll. 23 May 1992, molted 14 June (GES, PRM); nr. lake, 2♂, 13 June 1991 (PRM, GES); nr. entrance to park, pine litter, 14♂, 1 pr. ♂ & ♀, night, 13 June 1991. *Panola County*: Sandstone Nature Trail nr Sardis Dam, in uplands on ridge, 13♂, night, 13 July 1993 (GES, PRM, EAH). *Pontotoc County*: 1 mi SE Ecru, pitfall in deciduous woods, (4743-3,4), 2♂, 5 June 1980 (PRM); Natchez Trace Parkway, 1♂ in poor condition, kept in lab, 17 May 1983, 83–466 (WPM). *Tishomingo County*: Tishomingo St. Park, 3♂, 21 June 1991 (GES, PRM). *J.P. Coleman State Park*, oak pine woods along slope of a ravine, 2♂ 1♀, 24 June 1986 (GES). **TENNESSEE**: *Cumberland County*: Cumberland Mnt. State Park, deciduous woods, 1♂, night, 28 June 1983 (PRM). *Dixon County*: Montgomery Bell St. Park, uplands, oak-pine woods, 1♂, day, 29 June 1992 (GES). *Henderson County*: Natchez Trace St. Park, Fairview Gully's Trail nr. I-40, oak-pine litter, 3♂, day, 29 June 1992 (GES). *Marion County*: Foster Falls Wild Area of S. Cumberland St. Rec. Area, 10 mi S. of Tracey City, 3♂, 19 June 1992 (GES). *Shelby County*: Meeman Shelby State Park, uplands deciduous, at edge of woods, 3♂, 15 July 1996 (E. Grey, D. Wells, GES, PRM). *Wilson County*: Cedars of Lebanon State Park, Cedar Forest Loop Trail, hickory, oak, scattered cedar, 2♂, 15 May 1993 (GLM).



KEY TO MATURE MALES IN THE *SCHIZOCOSA OCREATA* GROUP

- 1a. Males with thick brush of black bristles on tibia of legs I, sometimes extending to the basal region of the tarsus (thickness of bristles makes it difficult to see tibia); apparent width of tibia (with bristles) from lateral view more than twice width of tibia alone . . . . . 2
- 1b. Males lacking thick brush of black bristles on tibia of legs I; may have some dark pigmentation or some dark hairs or may lack hairs and pigmentation on legs I . . . . . 3
- 2a. Paleal process with rugose prominence on retrolateral side (see Dondale & Redner 1978, Fig. 1; also Stratton 1991); tibial bristles extending to basal region of tarsus . . . . . *ocreata*
- 2b. Paleal process with smooth prominence along its retrolateral side (see Dondale & Redner 1978, Fig. 2; also Stratton 1991); bristles on tibia only . . . . . *crassipes*
- 3a. Males with dark pigmentation on tibia of legs I . . . . . 4
- 3b. Males lacking pigmentation on tibia and on femora . . . . . 5
- 4a. Males with dark pigmentation on tibia and on distal portion of femur . . . . . *stridulans*
- 4b. Males with pigmentation on tibia of legs I such that tibia is slightly darker than femur . . . . . *uetzi* new species
- 5a. Pale median band on cephalothorax with edges parallel . . . . . *rovneri*
- 5b. Pale median band on cephalothorax with edges scalloped . . . . . *floridana*

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## RESEARCH NOTE

### THE EFFECT OF HABITAT STRUCTURE ON WEB HEIGHT PREFERENCE IN THREE SYMPATRIC WEB-BUILDING SPIDERS (ARANEAE, LINYPHIIDAE)

The quality of a foraging site can have a significant effect on the survival, growth and reproductive success of web-building spiders (Riechert & Tracy 1975; Lubin et al. 1993; Ward & Lubin 1993). Consequently, web-spiders can be expected to be found most often in areas where prey is abundant. Some spiders, such as Linyphiidae or Agelenidae, construct more or less permanent and costly webs (Janetos 1982); and a movement to another web site involves both the desertion of the old web and a high energy investment in web construction at the new site (Janetos 1986). Thus, web site selection is a particularly important issue for these spiders (Janetos 1982).

Several factors may influence web site selection (Colebourn 1974; Uetz et al. 1978; Olive 1980; Brown 1981; Pasquet 1984). For example, spiders may select web sites in order to exploit specific prey types (Cherrett 1964; Uetz et al. 1978; Olive 1980; Ward & Lubin 1993) or to utilize the physical characteristics of a web site (Robinson 1981; Greenstone 1984; Pasquet 1984; Bishop & Connolly 1992; Ehmann 1994).

In the present study, web site selection in terms of web height was investigated for three sympatric linyphiid spiders, by testing whether the presence of a surrounding understory vegetation can influence the web height selected on young conifer trees. The studied spiders, *Frontinellina frutetorum* (C.L. Koch 1834), *Neriene radiata* (Walckenaer 1841) and *Linyphia triangularis* Clerk 1757 construct three-dimensional sheet webs consisting of a centrally located platform with barrier threads above to intercept flying prey, knocking them to the platform where the spiders hang waiting underneath. Voucher specimens of each species were deposited in the Arachnoidea collection, at the Natural History Museum Vienna, Austria.

The study was conducted in a mixed deciduous forest in eastern Austria, near Wörth an der Lafnitz, approximately 15 km from Hartberg (Styria). The study site (total area: 2854 m<sup>2</sup>) was comprised of plantations of Douglas fir (*Pseudotsuga menziesii*) and most webs were built on the young cultivated fir trees (Herberstein 1997). The study site was subdivided into four plots and fenced in to protect the trees from browsing animals. The fencing allowed a dense understory of grasses, ferns, raspberry and blackberry bushes to grow around the trees, which was cut every fall as part of forestry management.

An initial survey of web height (the distance from the ground to the sheet of the web) in 1993 (Herberstein 1997) suggested that web height was not constant throughout the year but increased as the season progressed. This trend was confirmed in 1994. Ten transects (10 × 1 m) were chosen each month (March–October) by randomly selecting the starting point and the direction (N, E, S, or W) of the transects which were allowed to intercept. Each inhabited web found along the transects was surveyed. There were significant positive correlations between web height (using individual data points) and time of the year for *F. frutetorum* ( $r = 0.47$ ,  $n = 152$ ,  $P < 0.01$ ), *N. radiata* ( $r = 0.48$ ,  $n = 224$ ,  $P < 0.01$ ), and *L. triangularis* ( $r = 0.27$ ,  $n = 287$ ,  $P < 0.01$ ) (Fig. 1).

At the same time as the spiders' web height increased, the vegetation surrounding the fir trees also increased in height, reaching its maximum height (Mean  $\pm$  SD = 1.05  $\pm$  0.33 m) in August/September. The observed change in web height may thus be a response to the growth of the understory, which overgrew web sites closer to the ground and reduced their attractiveness. Consequently, webs on trees lacking a surrounding understory are

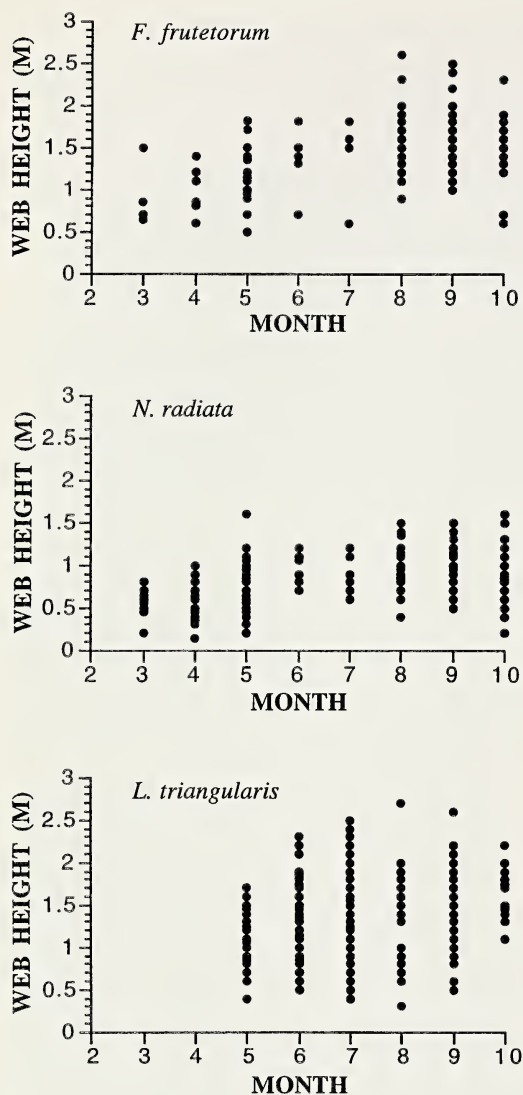


Figure 1.—The web heights are significantly correlated with time of the season for *Frontinellina frutetorum*, *Neriene radiata* and *Linyphia triangularis*.

expected to be placed closer to the ground compared to webs on trees surrounded by an understory. This assumption was tested during an experiment conducted from 10–15 August 1994 and from 2–13 September 1994.

Twenty firs were selected in close proximity (within an area of  $20 \times 20$  m), depending on the similarity of their height (mean  $\pm$  SD =  $2.03 \pm 0.09$  m), to reduce the effect of tree variability and habitat differences on web height selection. The trees were randomly allocated “control” or “experimental” trees.

The vegetation surrounding the 10 experimental trees was cut, leaving a clearance of 1 m in diameter, whereas the remaining 10 control trees were left in their natural condition, with a mature understory (maximum height: 1.2–1.5 m) surrounding them.

Before commencing the experiment, the 20 trees were surveyed twice (in the morning and the afternoon) and any spiders or webs on the trees were removed manually to avoid interference by other spiders, previously present on the trees. As spiders may be attracted to areas where silk is present (which may bias the results) the removal of spiders and web silk was carried out with great caution.

Immature *F. frutetorum* and *N. radiata* and adult *L. triangularis* were collected in the morning and marked on the abdomen with red, nontoxic paint. Twelve hours later, each spider was released onto the lowest branch (0.1–0.2 m from the ground) of each tree. Only a single spider was released per tree. The following morning the web height of each marked spider was measured, and the spiders and webs were removed.

As not all spiders responded by constructing a web, the entire procedure was repeated five times. The data sets were distributed normally (Kolmogorov-Smirnov Goodness of Fit tests) and differences in web height on trees with and without an understory were analyzed using one-tailed *t*-tests. Bonferroni's correction ( $\alpha' = \alpha/k$ , where *k* equals the number of non-independent tests) was used to analyze the results ( $P = 0.05/3 = 0.017$ ) in order to avoid inflation of the type I error probability.

Removing the shrub layer had a significant effect on the position of the webs. The web heights of *F. frutetorum* ( $t = 2.5$ ,  $df = 56$ ,  $P = 0.0073$ ), *N. radiata* ( $t = 3.05$ ,  $df = 58$ ,  $P = 0.0018$ ) and *L. triangularis* ( $t = 2.5$ ,  $df = 61$ ,  $P = 0.0081$ ) were significantly higher on trees surrounded by an intact understory than on trees without (Table 1). These results indicate that the vertical movement upwards may be a consequence of growing understory that either physically interferes with the spider webs, or reduces prey abundance to such an extent that the spiders desert their webs.

Spiders may re-locate their webs in response to food supply (Olive 1982; Vollrath 1985; Gillespie & Caraco 1987), disturbance (Hodge 1987b), support structure (Enders 1974; Hodge 1987a; Bradley 1993), variation



Table 1.—The average (mean ± SD) web heights of *Frontinellina frutetorum*, *Nerienne radiata* and *Linyphia triangularis* on trees with understory vegetation and without understory vegetation.

	Web heights (m) on trees	
	Understory intact (n)	Understory removed (n)
<i>Frontinellina frutetorum</i>	1.32 ± 0.30 (28)	1.10 ± 0.35 (30)
<i>Nerienne radiata</i>	0.79 ± 0.22 (27)	0.63 ± 0.21 (33)
<i>Linyphia triangularis</i>	1.52 ± 0.40 (32)	1.27 ± 0.38 (31)

in microclimatic conditions (Biere & Uetz 1981) or a combination of these factors. Spiders are unlikely to determine prey availability prior to web construction (Janetos 1986) or to use long term memory of site quality (Vollrath & Houston 1986). Thus, it seems unlikely that the web height selected by the spiders during the experiment is in direct response to prey abundance. Instead, the spiders might use microclimatic cues, which in turn may affect prey abundance.

The results of this experiment demonstrate that web placement in spiders is selective and can be influenced not only by the actual support structure utilized for web placement but also by the surrounding substrate such as a dense undergrowth.

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**RESEARCH NOTE**  
**ON SOME *CAMILLINA* FROM SOUTHERN AFRICA**  
**(ARANEAE, GNAPHOSIDAE)**

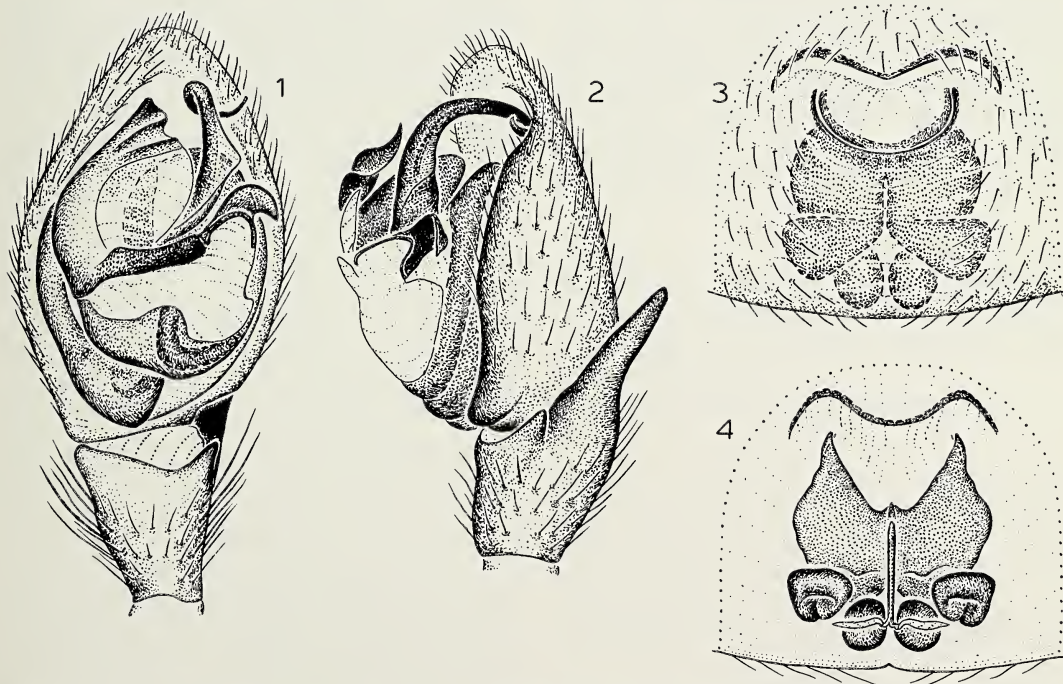
In Tucker's (1923) survey of the ground spider fauna of southern Africa, 12 species were assigned to the genus *Camillina* Berland 1919. Of those, four have already been transferred to other genera: *Camillina acanthognatha* (Purcell 1907) to *Trachyzelotes* Lohmander 1944 (by Platnick & Murphy 1984), *C. amnicola* Tucker 1923 to *Urozelotes* Mello-Leitão 1938 (by Platnick & Murphy 1984), and *C. browni* Tucker 1923 and *C. lutea* Tucker 1923 to *Setaphis* Simon 1893 (by Platnick & Murphy 1996). Of the others, *C. cordifera* (Tullgren 1910), *C. procurva* (Purcell 1908), and *C. biplagia* Tucker 1923 are currently considered valid species of *Camillina* (Platnick & Murphy 1987).

Thus, five of the 12 species have not yet

been treated in the modern literature. Through the courtesy of colleagues at the South African Museum in Cape Town, I've had the opportunity to examine the recently rediscovered types of three of those species.

One of these, *Camillina postrema* Tucker 1923, is represented by the male holotype from Diep River, Cape Flats, Cape Province, South Africa. It has the cheliceral bristles characteristic of *Trachyzelotes* and a palp characteristic of *T. jaxartensis* (Kroneberg 1875), a synanthropic and widespread species already recorded from South Africa. Like *C. acanthognatha*, *C. postrema* is here placed as a junior synonym of *T. jaxartensis* (NEW SYNONYMY).

A second species, *Camillina aestus* Tucker



Figures 1-4.—*Camillina setosus* Tucker. 1, Left male palp, ventral view; 2, Same, retrolateral view; 3, Epigynum, ventral view; 4, Same, dorsal view.

1923, is represented by the female holotype from Nompstsas, Namibia. The epigynum is not that of a *Camillina* species, but bears a series of transverse ridges. Similar ridges occur on the epigyna of two other species misplaced by Tucker in *Camillina*: *C. corrugata* (Purcell 1907) and *C. arida* (Purcell 1907). Accurate placement of these three species must await study of their males; they could represent an aberrant species group of *Zelotes* Gistel 1848, or perhaps even of *Urozelotes*. The latter possibility is an interesting one, as it would offer the first real clues about the relationships and geographic origin of the widespread, synanthropic species *U. rusticus* (L. Koch 1872). A revision of the African species of *Zelotes* will be required to clarify the relationships of this species group.

The third species, *Camillina setosus* Tucker 1923, is represented by one male and two female syntypes from Signal Hill, Cape Town, Cape Province, South Africa. Platnick & Murphy (1987) indicated that this species was probably a true member of *Camillina*, but the types could not then be located, and no other specimens could be assigned to the name on the basis only of Tucker's illustrations. Study of the now rediscovered syntypes indicates that this surmise was correct; *C. setosus* is a valid member of *Camillina*, known only from the type specimens. As was suggested by Tucker, *C. setosus* seems to be closest to *C. biplagia*; males share with that species a greatly elongated and sinuous embolus, but differ both in the shape of the embolus and of

the terminal apophysis (Figs. 1, 2; cf. Platnick & Murphy 1987, figs. 37, 38). Females of *C. setosus* can easily be distinguished from those of the other South African *Camillina* species by the widely separated posterolateral epigynal ducts (Figs. 3, 4).

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## RESEARCH NOTE

### A USEFUL PROCEDURE FOR ESTIMATING THE SPECIES RICHNESS OF SPIDERS

Many authors have noted that the abiotic structure of the environment is particularly important to spiders (Luczak 1963; Lowrie 1973; Stratton et al. 1978; Uetz 1979; Hatley & McMahon 1980; Bultman & Uetz 1983; Gunnarson 1983, 1992; Greenstone 1984; Rushton 1991; Sundberg & Gunnarson 1994; Moring & Stewart 1995). By and large, spiders are without the biochemical mandates characteristic of many organisms; for example, they are not bound to particular plant species as are many insects. Spiders are often exceptionally agile and in addition may occupy different aspects of their environment as they mature. It is suggested here that given the dominant role of the structure of the habitat, a simple saturation model might best be used to estimate the species richness of a habitat. Some of the assumptions relevant to the development of the model include: 1) Rarely collected spiders are largely a consequence of the vagility of spiders and reflect to some degree the size of the regional pool, the propinquity of other habitats, and the status of the populations of particular species at the time observations are made. For these reasons, species assemblages will tend to differ somewhat from year to year in any particular habitat (Rypstra & Carter 1995). 2) Spiders have fairly discreet requirements based on the spatial structure of the habitat and to a lesser degree on other factors such as humidity, temperature, light intensity, etc. (Rushton 1991; Morley & Stewart 1995). 3) Some species of spiders have different spatial requirements as they mature. 4) Within the regional pool there is a species assemblage that is adapted to a considerable degree to the niche-spatial options at any particular time offered by a habitat (more exactly, perhaps, the contained set of "microhabitats"). Spiders that are not suited to a particular habitat and wander in may soon leave or become prey for other organisms, including other spiders that are well

adapted to the habitat. 5) Combining samples taken in different years may lead to an overestimate of the number of species characteristic of any particular habitat as a result of the accumulation of records of species that result simply from the vagaries of vagility (Edwards 1997). As the model developed, it soon became apparent that it was analogous to the equation for adsorption isotherms created by Langmuir (1918).

It is postulated that within any habitat there is a set of  $n$  species or species-specific niches representing the maximum potential number of species in the habitat. At any time,  $n_q$  of these niches are occupied. When the habitat is saturated,  $n_q = n$ . The number of  $n$  potential and  $n_q$  occupied niches may vary with season, with the availability of other suitable habitats, and with changes in the regional pool (immigrants, introduced species, population changes both within and without the spider community that modify interactions, etc.).

Let  $n$  = total number of species-specific niches,

The rate of entry into the habitat:

$$dn_d/dt = k_a(n - n_q)q$$

where  $k_a$  = rate constant of arrival in the habitat and  $q$  = number of samples (quadrats). The rate of species entrance is proportional to the number of unoccupied niches, and to the sampling intensity.

The rate of species disappearance is:

$$-dn_d/dt = k_d n_q$$

where  $k_d$  = the rate constant of species disappearance. Rate of species disappearance is proportional to space already occupied. Departure may be voluntary, but includes other factors such as predation and disease.

Equating entry and departure (equilibrium):

$$k_a(n - n_q)q = k_d n_q \quad (1)$$

Taking reciprocals after setting equation equal to  $q$ :

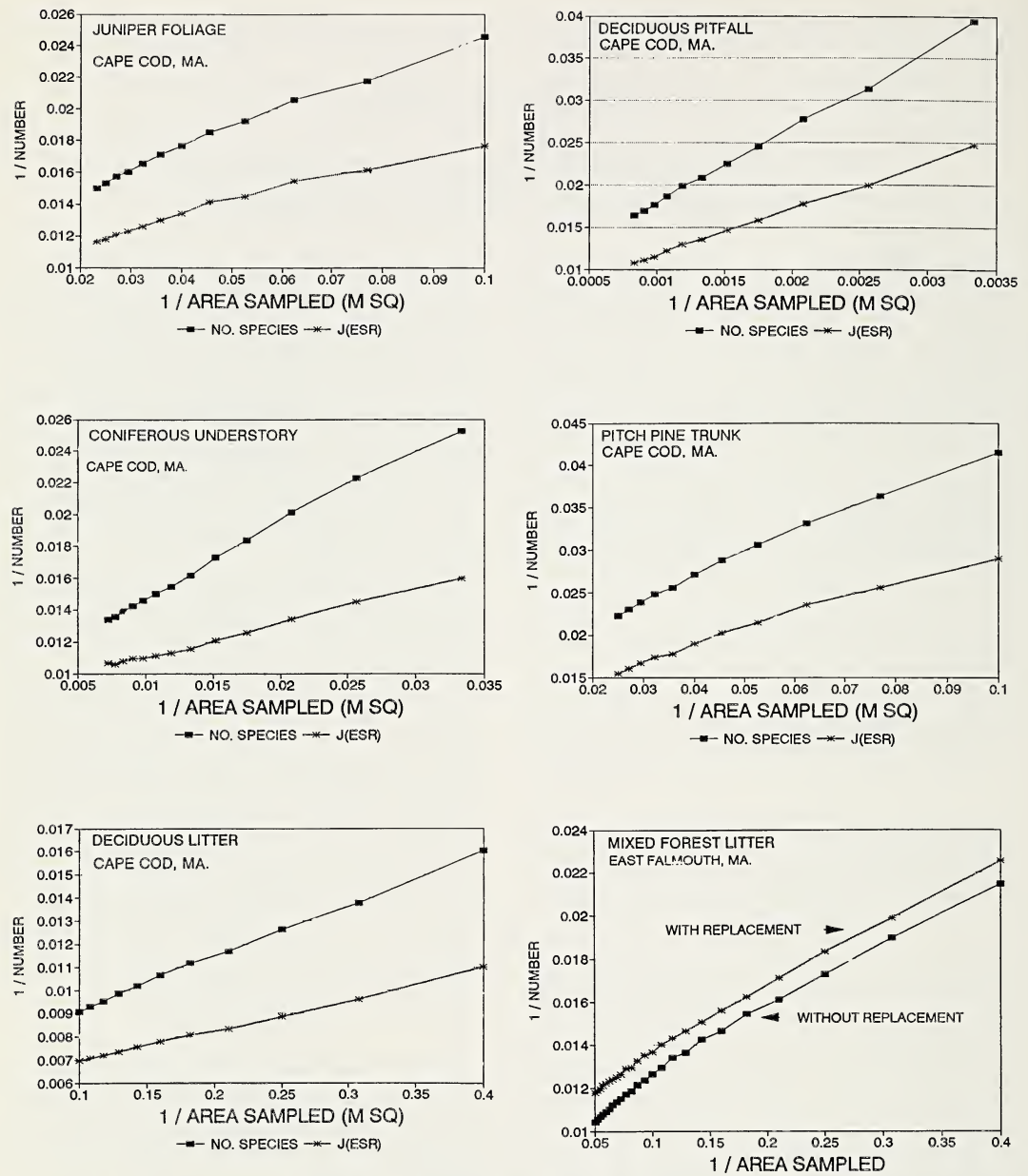


Figure 1.—Six examples of Cape Cod habitat data, with the reciprocals of the number of quadrats plotted against the reciprocals of the number of species collected and the reciprocals of the number of species calculated using the jackknife estimator. Each of these was sampled over a 3½ month period, 15 June–September 1989 and 1990.

$$1/q = k_a(n-n_q)/k_a n_q$$

Rearrangement gives:

$$1/n_q = [(k_d/k_a n)(1/q)] + 1/n \tag{2}$$

Note that a plot of  $1/nq$  against  $1/q$  is a straight line, with the slope =  $k_d/k_a n$  and the intercept =  $1/n$ . The reciprocal of the intercept

provides the estimated number of species,  $n(esr)$ , at saturation, and  $n = n_q$ .

In Figs. 1 and 2 both the number of species at saturation,  $n(esr)$  and the calculated number of species using the jackknife estimator,  $j(esr)$ , developed by Heltsche & Forrester (1983) are shown. The data were resampled randomly



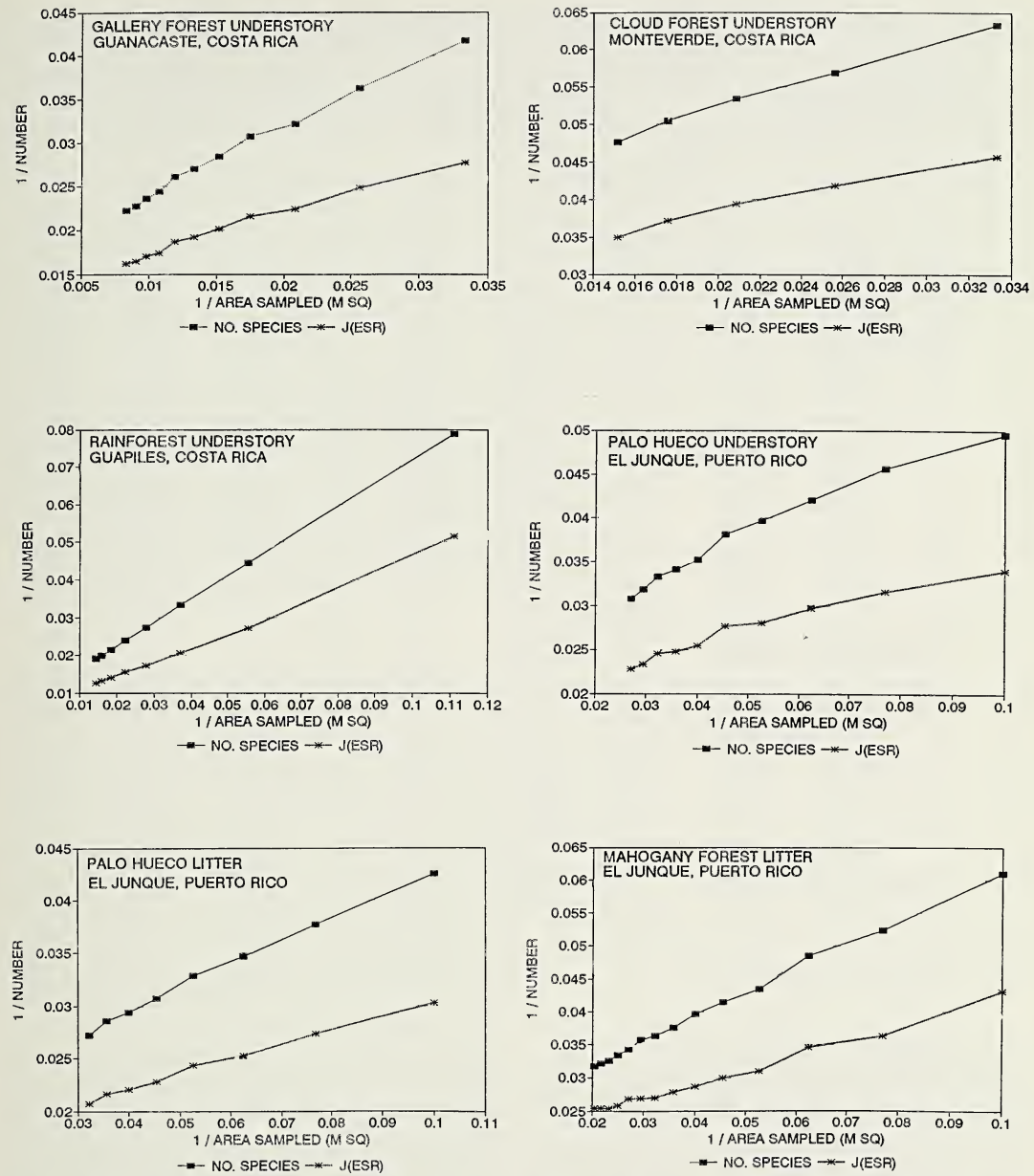


Figure 2.—Plots of the reciprocals of the number of quadrats against the reciprocals of the number of species and number of species calculated using the jackknife estimator for two examples from Costa Rica and four from El Junque, Puerto Rico. The Costa Rican samples were each collected in one day, while those from Puerto Rico were collected at intervals during 1994 and 1995.

without replacement, at three quadrat intervals beginning at 10 quadrats, with 100 iterations for each level of quadrat aggregation. The graphs are double reciprocal plots, with the number of quadrats shown on the abscissa and the number of species on the ordinate.

In Fig. 1, plots of the results of analysis for

six habitats from the Cape Cod region are presented. These are some of the habitats and collections reported on earlier (Edwards 1993). These habitats were sampled from the middle of June to the end of September, 1989–1990. In Fig. 2 data for various habitats in Puerto Rico and Costa Rica are plotted. The Costa

Table 1.—Statistical data for habitats using linear regression  $1/n_q = (x)(1/q) + c$  (Equation 5).  $q$  = number of quadrats,  $c$  = constant, SE = standard error,  $x$  = slope,  $n(esr)$  = estimated total number of species (reciprocal of  $c$ ),  $r_n^2 = r^2$  for calculations based on species,  $q_{50}$  = number of quadrats required to collect 50% of  $n(esr)$ ,  $j(esr)$  and  $r_j^2 = r^2$  for calculations based on number of species derived from jackknife estimator. Data in descending order of estimated total number of species  $n(esr)$ . For habitat codes see Table 2.

Code	$q$	$c$	SE $c$	$x$	SE $x$	$n(esr)$	$q_{50}$	$r_n^2$	$j(esr)$	$r_j^2$
CL	50	0.0062	0.0001	0.0899	0.0011	162.09	16.2	0.998	197.23	0.999
DL	41	0.0069	0.0001	0.0911	0.0013	144.91	14.1	0.998	177.38	0.998
CP	123	0.0077	0.0004	0.2122	0.0040	129.73	27.5	0.994	179.92	0.992
DP	41	0.0088	0.0003	0.3011	0.0039	113.25	34.1	0.999	160.23	0.999
XL	80	0.0093	0.0003	0.1277	0.0027	108.07	13.7	0.990	131.35	0.993
GP	52	0.0097	0.0005	0.2724	0.0055	103.07	29.0	0.995	140.31	0.992
DU	45	0.0098	0.0002	0.1037	0.0020	101.62	10.4	0.996	125.33	0.990
FP	43	0.0100	0.0002	0.2204	0.0022	100.16	21.9	0.999	123.82	0.996
CU	47	0.0100	0.0002	0.1560	0.0024	99.65	15.6	0.998	111.75	0.995
RU	23	0.0101	0.0002	0.2063	0.0007	99.31	20.5	1.000	158.73	0.997
FS	53	0.0112	0.0004	0.1198	0.0041	89.63	10.7	0.985	117.47	0.960
GS	45	0.0113	0.0006	0.1899	0.0075	88.18	17.0	0.985	130.04	0.984
PF	40	0.0115	0.0002	0.1422	0.0032	86.98	12.4	0.995	111.35	0.996
JF	44	0.0125	0.0003	0.1229	0.0035	79.76	9.8	0.992	99.59	0.979
DT	41	0.0149	0.0006	0.2856	0.0085	67.10	19.0	0.992	101.05	0.990
GU	40	0.0163	0.0005	0.2582	0.0069	61.37	15.9	0.994	78.65	0.988
CT	40	0.0165	0.0005	0.2575	0.0069	60.68	15.6	0.994	87.21	0.990
SF	25	0.0200	0.0002	0.1985	0.0031	50.08	10.4	0.998	61.82	0.996
HL	32	0.0206	0.0004	0.2224	0.0058	48.54	10.8	0.996	60.36	0.994
MU	71	0.0231	0.0010	0.2793	0.0100	43.35	12.1	0.976	56.38	0.967
ML	46	0.0244	0.0005	0.3688	0.0054	40.93	15.1	0.998	49.34	0.989
HU	39	0.0250	0.0010	0.2595	0.0143	39.97	10.4	0.976	51.38	0.967
BL	30	0.0256	0.0007	0.3337	0.0120	39.09	13.1	0.994	53.71	0.991
TL	61	0.0266	0.0005	0.3953	0.0048	37.53	14.8	0.998	41.99	0.967
BU	32	0.0271	0.0006	0.3408	0.0096	36.96	16.3	0.995	51.26	0.989
FU	14	0.0338	0.0019	0.1451	0.0090	29.63	4.3	0.992	45.52	0.996
VU	22	0.0355	0.0005	0.2790	0.0115	28.16	7.9	0.995	37.11	0.987
Means						15.5		0.993		0.988

Rican habitats were each sampled in one day. The Puerto Rican habitats show data collected at periodic intervals during 1994 and 1995.

The mean  $r^2$  values (Table 1) for the estimated number of species,  $n(esr)$ , against number of quadrats was  $r^2 = 0.9933$  (0.9761–0.9999), while the mean value of  $r^2$  for calculations based on the jackknife estimator,  $j(esr)$ , was  $r^2 = 0.9884$  (0.9597–0.9985). The slightly increased variability of the jackknife data is apparent to the eye in the figures. Estimates of  $j(esr)$  averaged about 31% more than  $n(esr)$ .

In some habitats there is an increase in the slope of the fitted line toward the origin, as may be seen in Fig. 1 for the red cedar foliage (JF) and in East Falmouth mixed forest leaf litter (XL). In Fig. 3, the skew ( $g_1$ ) and kur-

tosis ( $g_2$ ) of the frequency distribution of the numbers of species/quadrat in each habitat for the Cape Cod area is portrayed. The species assemblages of spiders are typically positively skewed and leptokurtic. The downward bend exhibited in some plots is evidence of the existence of a platykurtic and/or a multimodal distribution.

The sampling period for the Cape Cod habitats included at least part of the early fall onset of a different assemblage of species. The frequency distribution of the number of species for red cedar foliage (JF) is platykurtic and distinctly bimodal (Fig. 4a). Separating the data for the months of June-July from that for August-September resulted in the fitted lines shown in Fig. 4b. The second mode is interpreted as representing the incoming as-



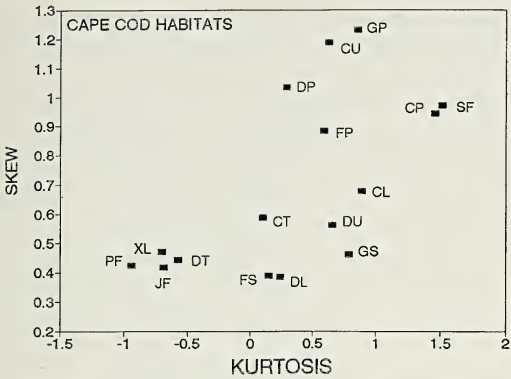


Figure 3.—The central moments, skew ( $g_1$ ) and kurtosis ( $g_2$ ) for the frequency distribution of the number of species/quadrat in Cape Cod habitats. Habitat codes are given in Table 2. A platykurtic distribution often indicates temporal change and/or environmental disturbance during the period of sampling. This is indicated by the increasing slopes in the red cedar foliage and mixed forest leaf litter data shown in Fig. 1.

semblage, with the vanishing summer assemblage contributing largely to the first mode. The  $n(esr)$  for this entire data set was 79.8 species ( $r^2 = 0.992$ ). The  $n(esr)$  for June and July was 62.3 ( $r^2 = 0.9999$ ) and for August and September was 74.7 ( $r^2 = 0.9971$ ). Similarly the pine foliage (PF) and deciduous trunk (DT) samples also suggested that seasonal change was involved. The East Falmouth mixed forest leaf litter (XL) data was more difficult to interpret. This habitat was sampled from January–March in 1993 (see Fig. 4c). By and large, the collection contained species to be expected in litter during the colder months. Also present was a fairly large number of arboreal species that could be considered the constituents of a second different assemblage, some or all individuals of which had taken refuge in the litter during the winter months.

Temporal change in the species assemblages during the period of sampling is a possibility that must be recognized. It should not, however, mitigate against comparable sampling from one year to the next providing relevant factors are kept constant.

Two examples of habitats sampled in Costa Rica are shown in Fig. 2. These habitats were each sampled in one day. The Puerto Rico samples were taken in the rainforest on El Junque during periodic visits from May 1994–

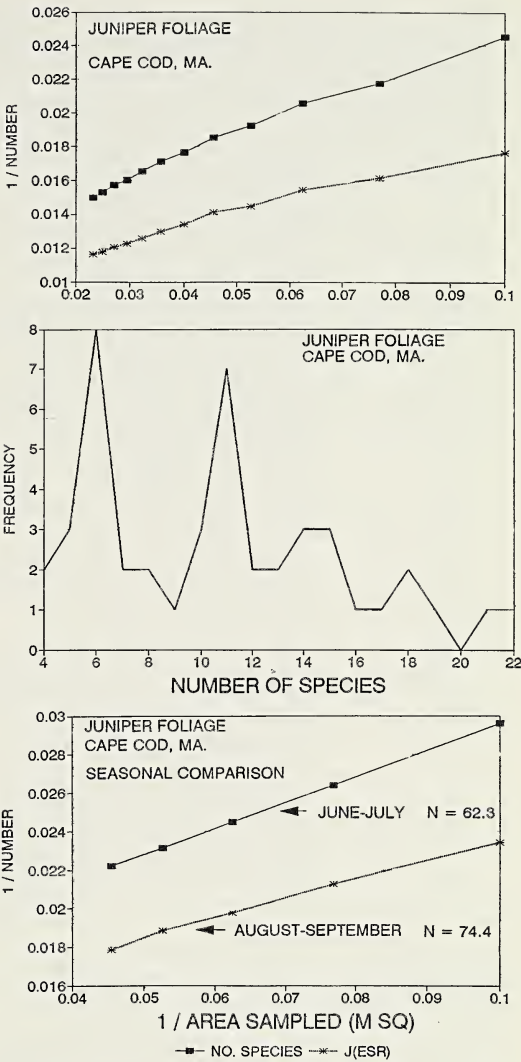


Figure 4.—4a, Frequency distribution of the number of species taken in red cedar (juniper) foliage (RF); 4b, Plot of the number of species for the period June–July, and the period August–September; 4c, The frequency distribution of species in the East Falmouth mixed forest leaf litter habitat (XL), collected January–March 1993.

March 1995 in the understory of a mahogany plantation (ML, MU) and September 1994–March 1995 in the leaf litter at Palo Hueco, a young mixed second forest area (HL, HU). During this period the area suffered a severe drought. This event may have contributed to some of the irregularity shown in the understory samples, although not in the leaf litter collections. An examination of the mahogany

Table 2.—List of codes used in Table 1, locality sampled, habitat, and estimated quadrat area and sampling method. CC = Cape Cod, CR = Costa Rica, PR = Puerto Rico (El Junque). For further details on sampling methods, see Edwards (1993).

Code	Locality	Estimated quadrat area
CL	Coniferous leaf litter, CC.	0.25 m <sup>2</sup> —sample
DL	Deciduous leaf litter, CC.	0.25 m <sup>2</sup> —sample
CP	Coniferous forest pitfall, CC.	±3.0 m <sup>2</sup> —sample
DP	Deciduous forest pitfall, CC.	±3.0 m <sup>2</sup> —sample
XL	Mixed forest leaf litter, CC.	0.25 m <sup>2</sup> —sample
GP	Grass field pitfall, CC.	±3.0 m <sup>2</sup> —sample
DU	Deciduous forest understory, CC.	2.4 m <sup>2</sup> —sweeping
FP	Old field pitfall, CC.	±3.0 m <sup>2</sup> —sample
CU	Coniferous understory, CC.	3.0 m <sup>2</sup> —beating
RU	Guapiles rainforest understory, CR.	3.0 m <sup>2</sup> —sweeping
FS	Old field foliage, CC.	10.0 m <sup>2</sup> —sweeping
GS	Grass field foliage, CC.	10.0 m <sup>2</sup> —sweeping
PF	Pine foliage, CC.	1.0 m <sup>2</sup> —beating
JF	Red Cedar foliage, CC.	1.0 m <sup>2</sup> —beating
DT	Oak trunk, CC.	1.0 m <sup>2</sup> —brushing
GU	Taboga Gallery Forest understory, CR.	10.0 m <sup>2</sup> —sweeping
CT	Pitch pine trunk, CC.	1.0 m <sup>2</sup> —bark removal
SF	Spruce foliage, CC.	1.0 m <sup>2</sup> —beating
HL	Palo Hueco mixed forest litter, PR.	0.25 m <sup>2</sup> —sample
MU	Mahogany forest understory, PR.	3.0 m <sup>2</sup> —sweeping
ML	Mahogany forest leaf litter, PR.	0.25 m <sup>2</sup> —sample
HU	Palo Hueco understory, PR.	3.0 m <sup>2</sup> —sweeping
BL	Mt. Britten Dwarf Forest leaf litter, PR.	0.25 m <sup>2</sup> —sample
TL	Tabonuco forest leaf litter, PR.	0.25 m <sup>2</sup> —sample
BU	Mt. Britten Dwarf Forest understory, PR.	3.0 m <sup>2</sup> —sweeping
FU	Guapiles rainforest fern understory, CR.	10.0 m <sup>2</sup> —sweeping
VU	Monteverde cloud forest understory, CR.	3.0 m <sup>2</sup> —sweeping

understory data showed some ambiguous evidence of seasonal change.

There is one further attribute of the saturation model that should be noted. At equilibrium (Equation 1), the number of quadrats needed under ideal circumstances to achieve 50% of the estimated number of species may be calculated. This is simply the reciprocal of the intercept/slope of Equation 2 (see Table 1,  $q_{50}$ ). In general, with the exception of the pitfall trap collections, when the number of quadrats reaches  $\pm 16$ , 50% of the estimated total number of species has been achieved (Table 1). In the case of pitfall traps, the number of quadrats needed to reach 50% is considerably more. Again, with the exception of pitfall trap collections, approximately 40 quadrats were necessary to achieve  $\pm 75\%$  of the estimated total number of species. The ground level is the principal route traveled by wandering spiders, thus pitfall traps provide a sample of the immediate habitat as well as a

sample of wandering spiders, especially adult males, from other habitats. The number of quadrats required to reach the  $q_{50}$  level (or any other desired level) is not directly determined by the number of species to be found in the habitat, or the number of quadrats, but rather by the rate at which additional species enter the collection. Within reasonable limits the size of the quadrat chosen should not alter the  $n(esr)$  although smaller quadrats are intuitively to be preferred, particularly where there is evidence of aggregation. The sampling method used and an estimate of the area sampled for the data presented here is provided in Table 2.

In summary, the data appear to be well fitted using a double reciprocal plot of the number of quadrats against the number of species. Simply using the number of species observed results in a relatively easy to understand estimate of species richness since there are no abstract mathematical considerations in-



volved. The procedure appears to be amenable to interpretation; that is, identifying and quantifying temporal change and other environmental changes. It is suggested that the jackknife estimator of Heltshe & Forrester (1983), an approach that involves giving weight to the number of unique species, will tend to overestimate the number of species. Combining samples taken in different years will result in an ever increasing overestimate of the species richness of a particular habitat, given the vagility of spiders.

The regional pool of spiders in the Cape Cod, Massachusetts area is estimated to be approximately 500 species (Edwards 1993). The results presented (see species estimates in Table 1) support the suggestion that specific Cape Cod habitats have a high beta diversity, are inhabited by interactive assemblages of spiders and tend to be saturated (Cornell & Lawton 1992; Edwards 1997).

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## RESEARCH NOTE

### A NOTE ON *EUSCORPIUS CARPATHICUS* (SCORPIONES, CHACTIDAE) FROM THE CRIMEA

*Euscorpius carpathicus* (L. 1767) (Chactidae), a scorpion species fairly common in southern Europe where it ranges from Spain to Ukraine, has been extensively studied (e.g., Birula 1917; Hadzi 1930; Caporiacco 1950; Vachon, 1963, 1975, 1978; Ćurčić 1972; Kinzelbach 1975; Fet 1986; Sherabon, 1987). There are 24 described subspecies; and, for most, the taxonomic status is unclear. Many of these forms are somewhat geographically isolated; for example, nearly every Mediterranean island (e.g., Mallorca, Sardinia, Sicily, Crete) has an endemic subspecies.

The Crimea Peninsula (currently an administrative territory within Ukraine) houses the easternmost, disjunct population of *E. carpathicus*. It is the only species of scorpion found in the Crimea. This population was first recorded from Alupka by Pallas (1795). It was described by C.L. Koch (1838) as *Scorpius tauricus* and for many years was treated as a separate, endemic species. Birula (1917) listed it as *Euscorpius tauricus* (C.L. Koch) and gave a detailed description of its anatomy and biology. Caporiacco (1950) synonymized it as a subspecies of *Euscorpius carpathicus* (L.). The original material from the Crimea has not been analyzed since 1917.

The studied sample included 71 specimens (17♂, 54♀) from the following localities of the Crimea Peninsula (area between 33–35°E and 44–45°N): Alushta, Balaklava, Frunzen-skoye, Gaspra, Inkerman, Kerch', Nikitsky Botanical Garden, Oreanda, Sevastopol', Sim-eiz, Simferopol', Sudak, Yalta, Yevpatoria. The studied specimens are deposited in the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia) and in the Zoological Museum of the Moscow State University (Moscow, Russia). Detailed label data are published in Fet (1989). The majority of this material originated from the Black Sea coast (southern parts of the peninsula), known for its mild climate due to the protection of

the Yaila range which runs latitudinally across the peninsula.

Following the technique developed for scorpions by Vachon (1963, 1975), I scored numbers of trichobothria on the pedipalp patella, which, in *Euscorpius*, vary both among and within local populations. Ventral trichobothria form a single row (Tv), whereas external ones appear in six clusters: terminal (*et*), subterminal (*est*), median (*em*), suprabasal (*esb*), and two basal groups (*eb<sub>a</sub>* and *eb*). There is no sexual dimorphism. Numbers may vary between left and right pedipalp, but such asymmetry is a subject of a separate study.

Trichobothrial numbers scored for the Crimean population were: Tv = 7 (20 cases, 14.3%), Tv = 8 (119 cases, 85.0%) and Tv = 9 (1 case, 0.7%) (number of scored pedipalps, 140); *et* = 5 (14 cases, 10.0%), *et* = 6 (126 cases, 89.4%) and *et* = 7 (1 case, 0.6%) (*n* = 141). Numbers of external trichobothria in other five groups did not vary and were: *est* = 4, *em* = 4, *esb* = 2, *eb<sub>a</sub>* = 4, *eb* = 4. Although some authors (Ćurčić 1972; Kinzelbach 1975) attempted to discuss clinal variation in trichobothria within *E. carpathicus*, few data are published that can be used for comparison to the population above. Kinzelbach (1975) gave an qualitative overview of many samples from the Balkan Peninsula and the Aegean Sea islands, using only the Tv index. He recognized not one but two species: an "oligotrichous" *E. carpathicus* (L.) with Tv = 7–8 and a "polytrichous" *E. mesotrichus* Hadzi with Tv = 10–12, which produce hybrid "mesotrichous" forms with Tv = 9–10. This division was not accepted by other authors (Vachon 1978; Fet 1986, 1989; Scherabon 1987).

The Crimean population has values of Tv close to 8 (mean Tv = 7.86,  $s^2$  = 0.13) and *et* close to 6 (mean *et* = 5.90;  $s^2$  = 0.10). Tv from 7–8 and *et* = 6 are found in certain populations from northeastern Greece (Kinzel-



bach 1975; Fet 1986). On the other hand, trichobothrial numbers of  $Tv = 9-10$  and  $et = 7$ , which are common throughout the Balkans and Crete (Fet 1986), are very rare ( $< 1\%$ ) in the analyzed Crimean sample. Populations of *E. carpathicus* farther westward are characterized by the forms with higher values of  $Tv = 10-12$ , and  $et = 7-8$ , e.g., in Austria (mean  $Tv = 10.25$ ,  $s^2 = 1.04$ ; mean  $et = 7.47$ ,  $s^2 = 0.38$ ; Scherabon 1987) or Sardinia (mean  $Tv = 11.01$ ,  $s^2 = 0.36$ ; mean  $et = 7.32$ ,  $s^2 = 0.67$ ; Vachon 1978). Means of trichobothrial scores of the Austrian and Sardinian populations are not significantly different;  $t$ -values are 0.93 for  $Tv$  ( $P > 0.5$ ) and 0.28 for  $et$  ( $P > 0.7$ ). However, the mean of the Crimean population significantly differs from a combined Austria/Sardinia sample (mean  $Tv = 10.67$ ,  $s^2 = 0.30$ ; mean  $et = 7.40$ ;  $s^2 = 0.40$ ). For this comparison,  $t$ -values are 6.85 for  $Tv$  ( $P < 0.001$ ) and 2.74 for  $et$  ( $P < 0.01$ ). According to Kinzelbach's (1975) terminology, the Crimean population is the *sensu stricto* "oligotrichous" *E. carpathicus* (L.).

The isolated zoogeographic position of this Crimean scorpion, and that of many Crimean animal and plant populations, is unique for the species' range: the closest populations of *E. carpathicus* are those in Romania, about 500 km westward. The reason for such disjunction should be sought in the paleogeographical history of the Crimea, which is relatively well studied (Golovach 1984). This area originated as an island of the Tethys Sea during the Mesozoic and throughout the Tertiary period was connected many times to different land masses (Caucasus, Balkan Peninsula, Anatolia, and/or modern Ukraine) when the sea regressed. There are no Tertiary relicts in the Crimea; and all endemic plants there are generally very recent (Grosset 1979). Severe Pleistocene glaciations in Europe (the last one, the Würm Ice Age, 70,000–11,000 years BP, corresponds to the Wisconsin of North America) could have eliminated most of ancient thermophile and mesophile Mediterranean species of the Crimea. Golovach (1984) analyzed the diplopod fauna in the Crimea, and suggested that its age is primarily Pleistocene and the source of migration was the eastern Mediterranean, especially the Balkan Peninsula. It can be suggested that the existence of *E. c. tauricus* is the result of a (possibly recent) migration from the Balkan Peninsula in the

Pleistocene interglacials. The source of such migration, then, should have been "oligotrichous" populations of eastern Balkans (with  $Tv = 7-8$  and  $et = 6$ ). Further comparative studies should assess the criteria for subspecific structure of *E. carpathicus*.

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(revised October 1996)

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbaktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 33, 34, *A-us y-us*, male. Scale = 1.0 mm.

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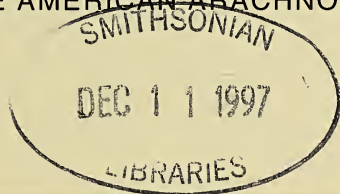
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# The Journal of ARACHNOLOGY

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*Cover illustration:* Photograph of *Phidippus audax* (Hentz) preying on a last instar noctuid corn earworm, *Helicoverpa zea* (Boddie). Photo by Clyde E. Morgan, USDA Agricultural Research Service (submitted by Matt Greenstone).

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Publication date: 21 October 1997



## SALTICIDAE OF THE PACIFIC ISLANDS. II. DISTRIBUTION OF NINE GENERA, WITH DESCRIPTIONS OF ELEVEN NEW SPECIES

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**ABSTRACT.** Pacific salticids of the genera *Ascyrtus*, *Bavia*, *Cosmophasis*, *Flacillula*, *Frigga*, *Ligurra*, *Plexippus*, *Thorelliola* and *Trite* are discussed. Eleven new species are described: *Ascyrtus similis*, *Ascyrtus rhizophora*, *Bavia fedor*, *Bavia sonsorol*, *Cosmophasis arborea*, *Cosmophasis lami*, *Cosmophasis muralis*, *Flacillula nitens*, *Ligurra opelli*, *Thorelliola dumicola* and *Trite ponapensis*. Illustrations and distribution records are presented for the new species. Drawings of four additional species of *Trite* are included.

This is the second in a series of papers on jumping spiders of the Pacific Islands (see Berry, Beatty & Prószyński 1996). In this paper we treat 24 species in the genera *Ascyrtus*, *Bavia*, *Cosmophasis*, *Flacillula*, *Frigga*, *Ligurra*, *Plexippus*, *Thorelliola* and *Trite*. Eleven new species are described from Fiji, Samoa and the Caroline Islands.

Several of the species included here have extensive distributions and have been reported many times before from the region: *Ascyrtus pterygodes* (L. Koch 1865), *Bavia aericeps* Simon 1877, *Bavia sexpunctata* (Doleschall 1859), *Frigga crocuta* (Taczanowski 1878) (mostly under the name *Sandalodes calvus* Simon 1902), *Plexippus paykullii* (Audouin 1825) and *Thorelliola ensifera* (Thorell 1877). At least three of these familiar species, sometimes more, can be found on most of the islands in the Pacific.

Except for Wanless's (1978) revision of the genus *Sobasina*, very little specifically on Pacific salticids has been published. Żabka (1987–1995) published a series of papers under the general title "Salticidae of Oriental, Australian and Pacific Regions". The emphasis of these publications is strongly on the fau-

nas of mainland Australia, Asia and the large continental islands, and little that is applicable to Micronesia and Polynesia is included. Berland (1934a) listed 40 salticid species from Polynesia, and in later papers (1934b, 1938, 1942) which included other Pacific areas, he added 15 more. Marples (1955a, 1955b, 1957, 1964) described six new species from Fiji, Tonga, Samoa and the Cook Islands. The New Guinea fauna described by Chrysanthus (1968) overlaps the fauna of the smaller oceanic islands only in the case of cosmotropical or widespread Pacific species (e.g., *Bavia aericeps* Simon 1877, *Menemerus bivittatus* (Dufour 1831), and *Plexippus paykullii* (Aud. 1825)).

The collections on which this paper is based were mostly made by J.W. Berry, E.R. Berry, and J.A. Beatty (indicated as JWB, ERB, and JAB in the text) in a series of collecting trips: Marshall Islands (1968, three months; 1969, three months); Palau (1973, six months); Guam, Yap, Truk, Ponape, Taiwan (1973, 1–2 weeks each); Yap (1980, six months); Marquesas, Tuamotu, Society, Cook and Fiji Islands (1987, six months total); and Hawaii (1995, one month). Specimens borrowed from



Map 1.—Major island groups in the Pacific Ocean.

the Bishop Museum (BPBM) and the American Museum of Natural History (AMNH) were also examined and are occasionally referred to in the text.

As in our previous paper, we have placed new species in previously described genera to which they are most similar, recognizing that they do not always match perfectly. For example, the species of *Trite* illustrated (Figs. 91–104) are genitally heterogeneous, though similar in habitus. A revision of the genus may very well dismember it and place the new species elsewhere.

Species limits within genera are, again, not narrowly defined. Small differences between Samoan and Fijian populations of *Ascyrtus similis* new species are conceived as intraspecific rather than interspecific variation (Figs. 12–16, 21–28). We feel that, before additional species are described, this variation should be investigated in more specimens than we have available.

None of the genera included here has been reported solely from the Pacific islands. *Ascyrtus*, *Frigga* and *Trite* are known from the Pacific islands and from Australia (*Frigga* from South America, also). *Flacillula*, *Ligura* and *Thorelliola* occur in the Pacific and in Asia (including Sri Lanka); while *Bavia* and *Cosmophasis* are found in the Pacific, Asia and Australia. *Plexippus* is cosmopolitan.

The generic diagnoses are intended to distinguish only among salticid genera reported from the Pacific Islands (Micronesia and Polynesia), excluding the large islands near Asia and Australia, the sub-Antarctic and the eastern Pacific Islands. In the descriptions the genera are categorized by size as follows: small, 2–4 mm total length; medium, >4–8 mm; large, >8–16 mm; and very large, over 16 mm. The anterior, middle and posterior eye rows are referred to, respectively, as eyes I, eyes II and eyes III. Illustrations of male palpi are of the left palp unless otherwise stated.

The holotypes and other specimens of all new species will be deposited in the Bishop Museum (BPBM) (State Museum of Hawaii) in Honolulu. All adult specimens are paratypes unless specifically excluded in the text; juveniles are not paratypes.

#### Genus *Ascyrtus* Karsch 1878

**Discussion.**—Seven species are currently listed in this genus (Žabka 1988; Prószyński 1990). All of these were described in the 19th or early 20th century, and most are poorly known and unrevised. Specimens mentioned in publications have almost all been identified as *A. pterygodes*. Species limits are not clear and the actual number of distinct species is unknown. Palpal structures are rather similar in all species.



**Diagnosis.**—Distinguishable from numerous other fissidentate Pacific genera especially by the antero-lateral “cheek” areas of the carapace, which are covered by iridescent scales. These areas are often broadened as well. They are usually detectable even in half-grown juveniles. Other diagnostic characters include the absence of lateral spines on first metatarsi, first coxae separated by more than the diameter of one of them, eyes in normal three rows instead of four (the second row midway between the first and third), pedicel concealed by abdomen in dorsal view, and cheliceral promargin in males with a large multicusped tooth.

**Descriptive notes.**—Medium to very large-sized fissidentate (bicuspid) salticids. Retrolateral surface of male chelicera with stridulatory grooves. Prolateral margin in males with a large multicusp tooth (4–6 cusps), in females a row of separate teeth. Antero-lateral portion of carapace expanded into broad, seta-fringed cheeks in males and some females. Male palps long and slender, especially the tibia; cymbium small, little wider than other palpal segments. Legs long and slender. Cephalothorax broad, flattened, squarish in appearance, usually with prominent cheeks laterally, fringed by setae and covered by reflective scales. Cheeks more pronounced in larger specimens, less so in smaller ones. Abdomen elongate, narrowing posteriorly, dorsal surface in males with a scutum, usually with indistinct edges; no scutum in females. Dorsum with two broad brown bands separated by a lighter median area; covered with adpressed colorless or brown scales. Face very low, reduced almost to the diameter of AME, but broad, clypeus very low. Chelicerae in males (and in female *A. pterygodes*) very large, diverging, elongate and broad, extended diagonally forward, covered with short setae. There is a bicuspid retrolateral tooth at midlength; a ridge on the retrolateral surface of the paturon ends in a tooth near the base of the fang. Prolateral tooth in some species preceded by an additional conical tooth; fang long. In females chelicerae usually of normal size, vertical, slightly bulging basally. Legs long and brown; tibiae I and II normally with 3–3 ventral spines, plus 2 to 3 prolateral and one retrolateral. Pedipalps thin and long.

*Ascyltus pterygodes* (L. Koch 1865)

Figs. 1, 4, 7, 9, 10, 11; Map 2

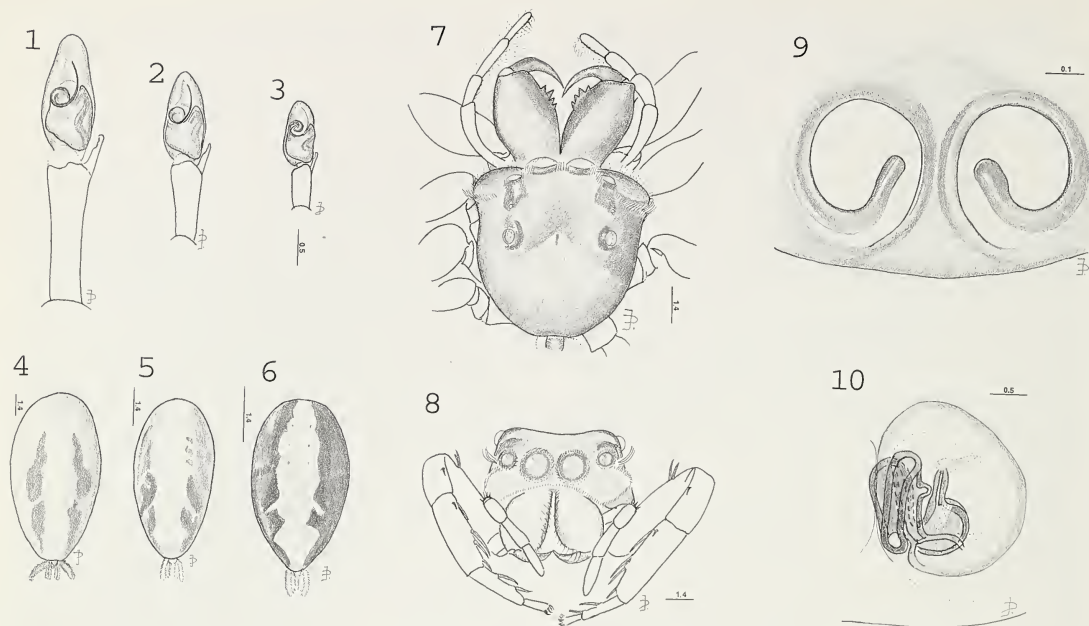
*Hyllus pterygodes* L. Koch 1865

*Ascyltus pterygodes* (L. Koch): Karsch 1878

**Diagnosis.**—Large to very large specimens; chelicerae large and divergent in both sexes. *Male*: Tibia of palp clearly longer than cymbium, fang furrow with transverse ridges, no diagonal ridge on anterior surface of chelicera. *Female*: Internal ducts of epigynum long, but not extending forward beyond “windows” (Figs. 10, 11), cheeks well developed.

**Description.**—*Male*: ( $n = 5$ ). Total length 13–19 ( $\bar{x} = 15.4$ ), length of carapace 5.5–7.0 ( $\bar{x} = 6.20$ ), maximum carapace width 5.1–6.9 ( $\bar{x} = 5.94$ ), eye field length 2.3–3.1 ( $\bar{x} = 2.77$ ), eye row I width 3.1–4.0 ( $\bar{x} = 3.58$ ). Cephalothorax brown, with eye field and ventral margins dark brown; cheeks very large and prominent. Abdomen brown with darker marginal streaks, sides brownish-grey, spinnerets dark greyish-brown. Frontal aspect—eyes I surrounded dorsally by orange setae, ventrally by white, chelicerae particularly broad, blackish brown, legs brown anteriorly. One bicuspid retrolateral cheliceral tooth plus a conical distal one offset somewhat from the fang furrow, one large five-cusped prolateral cheliceral tooth. Ventral aspect: mouth parts brown, endites with antero-external edges expanded triangularly, sternum light brown, medially lighter. *Legs*: Leg formula 1-2-4-3, patella-tibia III equal to IV. Patella-tibia I length 6.4–9.5 ( $\bar{x} = 7.84$ ). Coxae brown anteriorly and yellow posteriorly; abdomen ventrally greyish with brownish scales. *Palp*: With tibia distinctly longer than the cymbium (see Fig. 1).

*Female*: ( $n = 5$ ). Total length 16–20 mm ( $\bar{x} = 17.1$ ), length of carapace 5.5–7.0 ( $\bar{x} = 5.98$ ), maximum carapace width 5.1–6.5 ( $\bar{x} = 5.64$ ), eye field length 2.7–3.2 ( $\bar{x} = 2.81$ ), eye row I width 3.5–4.0 ( $\bar{x} = 3.69$ ). Cephalothorax brown like male, with eye field and ventral margins dark brown; cheeks very large and prominent, without vertical horn-like tufts of stiff black bristles near eyes II; chelicerae protruding forward, somewhat diverging, long (about  $\frac{1}{2}$  length of cephalothorax) and broad. Abdomen oval, swollen medially and narrowing posteriorly, but without scutum, covered densely with brownish scales on white back-



Figures 1-10.—Comparison of species of *Ascyltus*. 1-3. Ventral view of left palps all drawn to the same scale. 1, *A. pterygodes*; 2, *Ascyltus similis* new species; 3, *Ascyltus divinus*. 4-6. Abdominal patterns of females of *Ascyltus*, (drawn to different scales); 4, *A. pterygodes*; 5, *A. similis*; 6, *A. rhizophora*; 7, Dorsal view of cephalothorax of female *Ascyltus pterygodes*; 8, Frontal view of *A. rhizophora* new species; 9, *Ascyltus pterygodes* (L. Koch) epigynum; 10, Internal structure of *A. pterygodes* epigynum—single spermatheca and ducts.

ground, with two broad dark brown streaks of scales along posterior  $\frac{2}{3}$  of abdomen, divided by a narrow gap into two blocks; sides with mosaic of fine, dense brownish and whitish streaks of scales. Spinnerets brownish. Frontal aspect: much like male, eyes I surrounded dorsally and ventrally by orange setae, chelicerae blackish-brown covered with short sparse whitish setae. One bicuspid retrolateral cheliceral tooth, six prolateral cheliceral teeth. Ventral aspect: as in male, except endites with antero-external edges rounded, sternum light brown, medially lighter; coxae brownish yellow; abdomen ventrally very light brownish. *Legs*: Leg formula 4-3-1-2, patella-tibia III equal to IV. Patella-tibia I length 5.1-7.8 ( $\bar{x}$  = 6.14). Legs light brown, the first pair darker. *Epigynum*: With septum narrow at mid-length, internal duct with double loop about half as long as diameter of "window" or slightly more (see Figs. 9, 10).

**Material examined.**—**FIJI**: Viti Levu, Nandarivatu, in house, 1♂, 11 April 1987 (JAB); Nandarivatu, along stream near swimming pool, 1♂, 12 April 1987 (JWB); Nandarivatu, on shrub at swim-

ming pool, 1♂, 12 April 1987 (JAB); Nandarivatu, at swimming pool, 1♀, 14 April 1987 (JAB); Nandarivatu, in house, 1♂, 17 April 1987 (JAB). **HAWAII**: Hawaii County, Captain Cook, on bush in nursery, 1♂, 15 January 1988; Manuka State Park, mesic forest, elev. 1770 ft., 2♀ 13mm, 11 February 1995; Kalopa State Park, shaking banana leaves, elev. 2500 ft., 1♂ 3♀ 8mm; Waipio Valley Lookout, on clay bank, 1♂, 14 February 1995; Lapahoe, elev. 500 ft., shaking banana leaves, 1♂ 12mm, 20 February 1995; Lapahoe, elev., 1100 ft., along gulch, 1♂ 11mm, 20 February 1995; Isaac Hale Beach Park, *Pandanus* litter, 1♀ 2mm, 23 February 1995. (All Hawaiian specimens collected by J.W. & E.R. Berry.)

**Distribution.**—Reported from Hawaii, Samoa, Fiji, Tonga, Niue, the Ellice, Tokelau, New Hebrides, Loyalty and Society Islands.

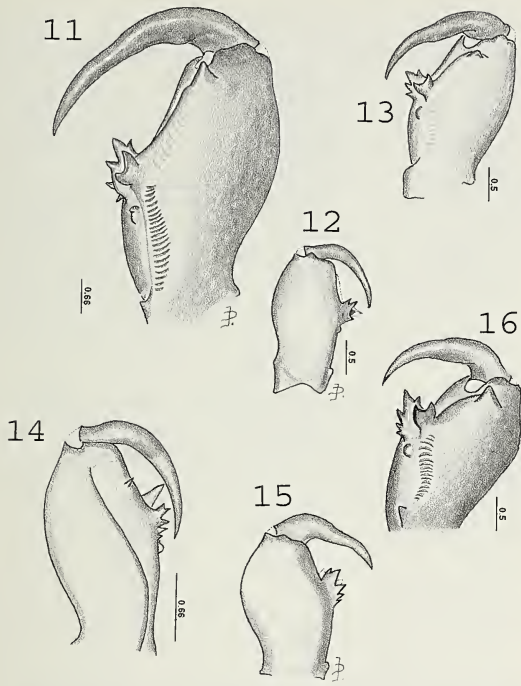
*Ascyltus divinus* Karsch 1878

Figs. 3, 14, 17-20; Map 2

*Ascyltus simplex* Karsch 1878: synonymized by Zabka (1988)

**Discussion.**—Zabka's (1988) drawing of the male chelicerae shows a simple prolateral tooth, not the multicusp tooth typical of the





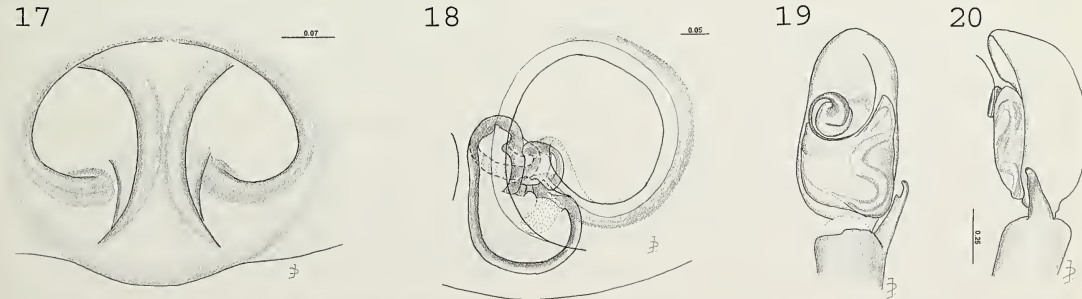
Map 2.—Distribution of four species of *Ascyltus* in the Pacific. *Ascyltus pterygodes* (\*), *Ascyltus divinus* (Δ), *Ascyltus similis* new species (□), *Ascyltus rhizophora* new species (◇).

Figures 11–16.—Comparison of chelicerae in males of several *Ascyltus* species. 11, Ventral view in *Ascyltus pterygodes* from Fiji; 12, Dorsal view in *Ascyltus similis* new species from Samoa; 13, Ventral view in *Ascyltus similis* new species from Samoa; 14, *Ascyltus divinus* from Fiji [cf. Zabka 1988: 424–427, fig. 8]; 15, Dorsal view of chelicera of *Ascyltus similis* new species from Fiji; 16, Ventral view of chelicera in *A. similis* new species from Fiji.

imens match Žabka’s description and illustrations well. Apparent differences in the females are attributed to individual variation, different styles of drawing and differences in the condition of the specimens. As the males of no other species have an anterior ridge on the chelicera, we include our specimens in *A. divinus*.

**Diagnosis.**—Male chelicerae with sparse inconspicuous setae dorsally, with prominent diagonal sclerotized ridge, cusps of prolateral tooth small, running down one edge of tooth. Fang furrow with transverse ridges. Internal ducts of epigynum short, cheeks of female not expanded or rimmed by long setae.

**Description.**—*Male*: ( $n = 3$ ). Total length 7.9–8.6 ( $\bar{x} = 8.19$ ), length of carapace 3.3–3.6 ( $\bar{x} = 3.50$ ), maximum carapace width 2.9–3.4 ( $\bar{x} = 3.08$ ), eye field length 1.7–2.0 ( $\bar{x} = 1.91$ ), eye row I width 2.4–2.7 ( $\bar{x} = 2.54$ ). Cephalothorax yellowish-brown with eye field light brown, cheeks present but not prominent. Abdomen brownish-yellow, sides whitish,



Figures 17–20.—*Ascyltus divinus* Karsch. 17, Epigynum; 18, Internal structure of epigynum showing single spermatheca and ducts. 19, Left palp, ventral view; 20, Left palp, lateral view.

spinnerets light brown. Frontal aspect—eyes I surrounded by indistinct whitish setae, some with slightly orange shade, chelicerae with prominent black sclerotized ridge on anterior surface, anterior legs yellow. One proximal bicus, plus two low conical (one proximal to bicus and one distal to bicus) retrolateral teeth; one large 5-cusped prolateral cheliceral tooth (plus another conical one more distal). Ventral aspect: mouth parts brown, endites with antero-external edges rounded, sternum light brown, medially lighter; coxae yellow; abdomen ventrally whitish with four indistinct longitudinal lines of brownish spots. *Legs*: Leg formula 1-2-4=3, patella-tibia III equal to IV. Patella-tibia I length 4.3–6.0 ( $\bar{x}$  = 5.23). Legs yellow, spination of tibia I differs from the remaining species by lateral spines being only indistinctly shortened and presence of similar spines on retro-lateral surface as well, the same spination appears on tibia II. Palpal structures not distinctive.

*Female*: ( $n$  = 5). Total length 7.5–8.3 ( $\bar{x}$  = 7.91), length of carapace 2.6–3.4 ( $\bar{x}$  = 3.21), maximum carapace width 2.0–2.8 ( $\bar{x}$  = 2.55), eye field length 1.3–1.8 ( $\bar{x}$  = 1.67), eye row I width 2.0–2.4 ( $\bar{x}$  = 2.27). Differs from other *Ascyrtus* by absence of distinct cheeks, the cephalothorax here is as broad as under eyes III, but not broader. Cephalothorax with eye field fawn, an indistinct pattern of longer and broader whitish scales along midline, along posterior edge and along lateral eyes, surrounding two spots of light brownish scales; rims of eyes I covered dorsally with longer whitish scales, a few longer orange scales between AME. A whitish diamond-shaped area behind eye field followed by slightly darker, light fawn middle thorax with sparse orange setae, lower thorax and sides whitish. Abdomen whitish, with sparse widely spaced orange scales and also scattered dark, upright short bristles; no pattern visible. Frontal aspect: eyes I surrounded with white setae with an indistinct dot of orange setae laterally and medially, AME surrounded by light brown area, very thin laterally and ventrally, whitish area under ALE, expanded laterally but not making any extended plate, rimmed dorsally by a diagonal line of small whitish scales, followed laterally by a line of red scales running from ALE sideways. Clypeus with thin line of horizontal whitish setae. Chelicerae vertical and slightly diverging, bulging basally, yellow,

low, their length being about twice diameter of AME. One bicus retrolateral cheliceral tooth, four prolateral cheliceral teeth. Pedipalps whitish, with long white setae. Ventral aspect: generally whitish, chelicerae and mouth parts yellow. *Legs*: Leg formula 4-3-1-2; patella-tibia III equal to IV. Patella-tibia I length 2.0–2.9 ( $\bar{x}$  = 2.60). Legs yellowish dorsally with prominent brown spines, ventrally whitish. *Epigynum*: With septum broad at mid-length, internal duct short, inconspicuously looped (see Figs. 17, 18).

**Material examined.**—**FIJI**: *Viti Levu*, mangrove swamp by road near Namuka Harbor, sweeping, 1♀, 2 May 1987 (JWB & ERB). Nandarivatu, elev. 900 m, tree shaking in shrubs, 1♀, 11 April 1987 (JWB & ERB). Namosi Road, 7.7 km north of Queen's Road, roadside sweeping & shaking, 2♀ 2imm, 7 May 1987 (JAB, JWB & ERB). Lomaivuna Distr., 3 km N of Nanggali, tree shaking, in pine, 1♂ 1♀ 1imm, 30 May 1987 (JWB & ERB). Namosi District, hilltop forest about 7 km N of Queen's Road on Namosi Road, 1♂, 19 May 1987 (JWB & ERB). Nausori Highlands, forest reserve Koronsingalevu Block, elev. 1500 ft., sweeping & shaking, 1♂, 27 May 1987 (JWB & ERB).

**Distribution.**—Reported only from Fiji and Australia (Żabka 1988).

#### *Ascyrtus similis* new species

Figs. 2, 5, 12, 13, 15, 16, 21–28; Map 2

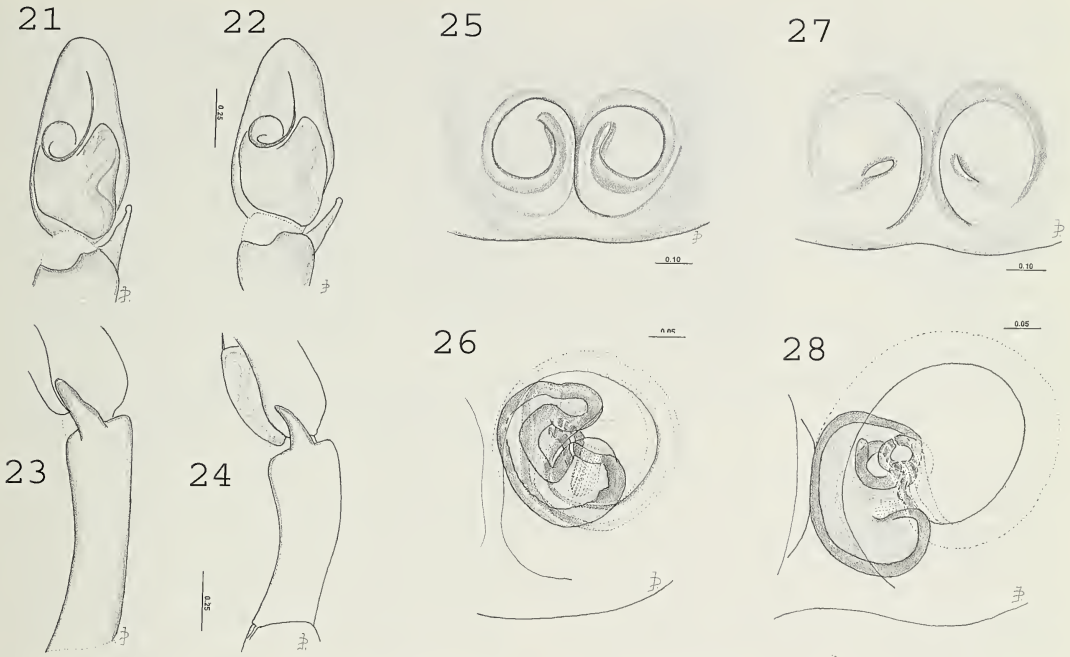
**Holotype.**—Male from Fiji: Viti Levu, 7 mi. N of Singatoka, sweeping and shaking bushes along river bank, 21 May 1987. (J.W. & E.R. Berry) (BPBM).

**Etymology.**—The name *similis*, similar, refers to the resemblance of this species to *A. pterygodes*.

**Diagnosis.**—Smaller than *A. pterygodes*, which it resembles. Male chelicerae lacking dorsal sclerotized ridge, fang furrow with only slight transverse ridges. Females with seta-rimmed cheeks. Epigynum with short internal ducts. Tibia of male palp only a little longer than cymbium.

**Description.**—*Male*: ( $n$  = 3). Total length 8.0–11.5 ( $\bar{x}$  = 9.57), length of carapace 4.4–5.2 ( $\bar{x}$  = 4.71), maximum carapace width 3.9–4.5 ( $\bar{x}$  = 4.08), eye field length 2.3–2.5 ( $\bar{x}$  = 2.38), eye row I width 2.9–3.0 ( $\bar{x}$  = 2.96). Cephalothorax brown, with eye field and ventral margins dark brown, cheeks very large and prominent. Abdomen with scutum brown, margins and sides lighter brownish grey.



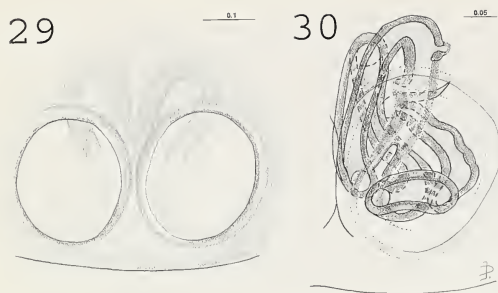


Figures 21–28.—*Ascyrtus similis* new species. Comparison of left palps and epigyna for specimens from Fiji and Samoa. Comparable structures are drawn to the same scale. 21, Palp, ventral view (Fiji); 22, Palp, ventral view (Samoa); 23, Palpal tibia, lateral view (Fiji); 24, Palpal tibia, lateral view (Samoa); 25, Epigynum (Fiji); 26, Internal structure of epigynum (Fiji); 27, Epigynum (Samoa); 28, Internal structure of epigynum (Samoa).

Frontal aspect: eyes I surrounded dorsally by orange setae, ventrally by white; chelicerae broad, blackish-brown, legs brown anteriorly. Retrolateral cheliceral teeth: one bicus, plus two low rounded bumps, one proximal and one medial to the bicus tooth; one four-cusped prolateral cheliceral tooth. Ventral aspect: mouth parts brown, endites with antero-external edges expanded triangularly, sternum light brown, medially lighter; coxae brownish-yellow; abdomen greyish ventrally with brownish scales. *Legs*: Leg formula 1-2-4-3; patella-tibia III equal to IV. Patella-tibia I length 4.9–5.7 ( $\bar{x}$  = 5.27). *Palp*: Structures as in *A. pterygodes* except for proportionately shorter tibia.

*Female*: ( $n$  = 5). Total length 9.8–12.6 ( $\bar{x}$  = 11.40), length of carapace 4.1–5.3 ( $\bar{x}$  = 4.79), maximum carapace width 3.3–4.5 ( $\bar{x}$  = 3.96), eye field length 2.0–2.7 ( $\bar{x}$  = 2.44), eye row I width 2.7–3.4 ( $\bar{x}$  = 3.08). Cephalothorax as brown as in male, with eye field and ventral margins dark brown; cheeks large and prominent, vertical horn-like tufts of stiff black bristles near eyes II, chelicerae not pro-

truding forward. Abdomen narrowing posteriorly, without scutum, with remnants of two intensely brown lateral streaks of narrow scales along posterior  $\frac{2}{3}$  of abdomen, extended anteriorly by greyish scales, divided into three blocks by narrow gaps, median longitudinal area whitish with colorless scales; sides whitish covered with colorless scales. Spinnerets brownish. Frontal aspect: eyes I surrounded dorsally by orange setae, no surrounding setae ventrally, but with a few dark setae along edge of clypeus, and dense short whitish setae on bases of chelicera make a white line under AME; chelicerae bulging basally but directed vertically, much smaller than in male, light brown, covered with short and sparse whitish setae. One bicus retrolateral cheliceral tooth, four prolateral cheliceral teeth. Ventral aspect: mouth parts brown, endites with antero-external edges rounded, sternum yellowish; coxae yellowish; abdomen ventrally whitish. *Legs*: Leg formula 1-3=4-2; patella-tibia III shorter than IV. Patella-tibia I length 3.6–5.2 ( $\bar{x}$  = 4.51). Legs brown ante-



Figures 29–30.—*Ascyrtus rhizophora* new species from Fiji. 29, Epigynum; 30, Internal structure of epigynum showing single spermatheca and ducts.

riorly. *Epigynum*: See diagnosis and Figs. 25–28.

**Material examined.**—**FIJI**: *Viti Levu*, Suva, Lami Beach, on shrub foliage, 1♀, 3 May 1987 (JAB & ERB). Seven mi. N of Singatoka, sweeping & shaking bushes along river bank, 1♂1♀, 21 May 1987 (JWB & ERB); **AMERICAN SAMOA**: *Tutuila*, Fagatogo, 2♂1♀1imm, 13 July 1973 (JAB); 3♀5imm, 14 July 1973 (JAB).

**Distribution.**—Known only from Fiji and American Samoa.

*Ascyrtus rhizophora* new species

Figs. 6, 29; Map 2

**Holotype.**—Female from Fiji: *Viti Levu*, near Namuka Harbor, mangrove swamp, sweeping, 2 May 1987, (J.W. & E.R. Berry) (BPBM).

**Etymology.**—A noun in apposition after the mangrove genus *Rhizophora*.

**Diagnosis.**—Female with long internal epigynal ducts that loop forward beyond anterior margin of “windows”. With seta-rimmed cheeks.

**Description.**—*Male*: Male is unknown.

*Female*: ( $n = 1$ ). Total length 8.7, length of carapace 4.0, maximum carapace width 3.2, eye field length 1.9, eye row I width 2.6. Resembles other *Ascyrtus* by small cheeks, extended by rims of bent setae; rims of eyes I covered dorsally with reddish setae. Cephalothorax whitish, with eye field anteriorly dark brownish-grey. Very indistinct, small, transparent adpressed scales, colorless and light brown; posterior median whitish area on eye field is continued as median broad whitish belt along the whole length of thorax, limited on both sides by broad darker belts, consisting of small grey spots and covered with semi-trans-

parent brownish scales; sides whitish covered in upper parts by sparse brownish scales, lower sides whitish, limited by the thin dark brown line on the ventral edge. Abdomen with distinct reddish-brown pattern on whitish background (Fig. 6). Frontal aspect: eyes I surrounded with orange-red setae, face appears light greyish-brown, due to scales and setae on pale tegument; cheek plates small but broader than cephalothorax behind them, covered by adpressed brownish-grey, shiny setae, rimmed laterally by a thin indistinct line of white setae, dorsally by a diagonal line of red scales running from ALE sideways. Clypeus obsolete, with a thin line of horizontal whitish setae. Chelicerae vertical and slightly diverging, bulging basally, yellow, their length being about twice diameter of AME. Pedipalps whitish, with long white setae and a spot of brownish scales on patella. One retrolateral cheliceral tooth, four prolateral cheliceral teeth. Ventral aspect: generally whitish, chelicerae and mouth parts yellow. *Legs*: Leg formula 4-3-1-2, patella-tibia III equal to IV. Patella-tibia I length 3.8. Legs dorsally yellowish with indistinct darker rings and prominent brown spines; ventrally whitish. *Epigynum*: See diagnosis and Figs. 29, 30.

**Material examined.**—**FIJI**: only the holotype.

**Distribution.**—Known only from Fiji.

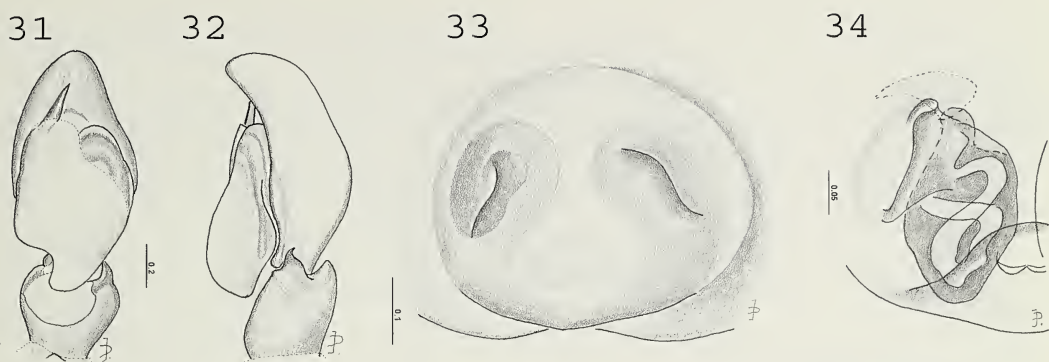
Genus *Bavia* Simon 1877

**Discussion.**—Prószyński (1990) catalogs 12 species of *Bavia*, occurring from the Philippines and southeast Asia to Australia. Five of these have recently been discussed by Žabka (1988), who questions the placement of *B. annamita* Simon 1903 and *B. thorelli* Simon 1903 in the genus. We describe two additional species.

**Diagnosis.**—Distinguishable from the few other pluridentate genera in the Pacific (*Lagnus* L. Koch 1879, *Myrmarachne* MacLeay 1838 and *Lepidemathis* Simon 1903) by having the pedicel concealed by anterior part of abdomen, coxae II and III not more widely spaced antero-posteriorly than other coxae, cephalothorax low, relatively flat and strongly convex laterally, ocular quadrangle parallel-sided, cheliceral retromargin with 6–7 small, acute contiguous teeth, promargin with three larger teeth, the middle one the largest.

**Descriptive notes.**—Medium-to-large pluridentate salticids with low broad carapace,





Figures 31–34.—*Bavia aericeps*. 31, Left palp ventrally; 32, Palp laterally; 33, Epigynum; 34, Internal structure of epigynum showing left spermatheca and ducts.

elongate, narrow abdomen broadest anteriorly and narrowing to posterior end, with long spinnerets. Endites much longer than wide, often abruptly expanded distally. First pair of legs longest, more robust and darker in color than other legs. Tibia with ventral spines in two rows of three each, metatarsi with 2–2 ventral spines in distal half. First legs and carapace reddish-brown, with spots or short streaks of light colored scales on carapace. Other characters as in diagnosis and species descriptions.

*Bavia aericeps* Simon 1877

Figs. 31–34, 45; Map 3

*Bavia aericeps* Simon 1877; Žabka 1988b.

*Acompse suavis* L. Koch 1879; Keyserling 1883.

**Description.**—*Male*: ( $n = 5$ ). Total length 8.4–11.3 ( $\bar{x} = 10.16$ ), length of carapace 3.5–4.9 ( $\bar{x} = 4.14$ ), maximum carapace width 2.4–3.9 ( $\bar{x} = 3.10$ ), eye field length 1.6–2.3 ( $\bar{x} = 1.98$ ), eye row I width 2.0–2.6 ( $\bar{x} = 2.24$ ). Cephalothorax reddish-brown, lighter dorsally, eye field dark brown, followed by transverse whitish spot, a few small colorless setae along lateral eyes and a row of long brown and reddish bristles above eyes I; posterior slopes of thorax and sides with few erect black setae, a few white spots on posterior thoracic slope. Abdomen with three longitudinal streaks: the median one whitish, the two marginal ones darker, weakly brownish-violet in alcohol, followed by three pairs of small spots; a thin marginal whitish line anteriorly, expanding into whitish sides; spinnerets light brownish-grey. Face brown with dense white clypeal “mustache”, eyes I surrounded by indistinct reddish setae. Diameter of AME = 2.5

diameters of ALE. Six retrolateral cheliceral teeth, three prolateral cheliceral teeth. *Legs*: Leg formula 1-4-2-3, patella-tibia III shorter than IV. Patella-tibia I length 3.0–5.2 ( $\bar{x} = 3.96$ ). Femur and tibia I with inconspicuous spots of whitish setae prolaterally in middle of patella and apex of tibia. Tarsus I light yellow. Endites elongate with a rectangular elongate expansion along external edge. Chelicerae posteriorly brown, endites, labium and anterior coxae light greyish-brown, coxae III–IV whitish-yellow; sternum yellow, brown rimmed; abdomen ventrally greyish-white with light brown, sclerotized epigastric fold, grey rectangular area in the posterior third of abdomen, spinnerets surrounded by a narrow dark ring. *Palp*: Embolus short and straight (Figs. 31, 32). Pedipalps light brownish-grey, without contrasting spots, with longer dark setae along prolateral edge of cymbium and tibia.

*Female*: ( $n = 5$ ). Total length 9.7–12.5 ( $\bar{x} = 10.70$ ), length of carapace 4.3–4.9 ( $\bar{x} = 4.62$ ), maximum carapace width 3.3–3.9 ( $\bar{x} = 3.56$ ), eye field length 2.1–2.4 ( $\bar{x} = 2.20$ ), eye row I width 2.3–2.6 ( $\bar{x} = 2.40$ ). Colors as in male, except behind eye field there is a whitish transverse area with fovea in the middle, pedipalps with flattened dorsal surfaces, yellow, medially dark brown, framed laterally with dense fringes of white, short setae. Six retrolateral cheliceral teeth, three prolateral cheliceral teeth. Endites elongate, externally broadened and rounded, without depression or expansion. *Legs*: Leg formula 1-4-2-3, patella-tibia III shorter than IV. Patella-tibia I length 3.3–3.8 ( $\bar{x} = 3.57$ ). *Epigynum*: With openings widely separated, posterior margin



Map 3.—Distribution of four species of *Bavia* in the Pacific. *Bavia aericeps* (\*), *Bavia sepxunctata* (■), *Bavia fedor* new species (□), *Bavia sonsorol* new species (△).

projecting in midline, internal duct relatively wide (Figs. 33, 34).

**Material examined.**—**COOK ISLANDS:** *Rarotonga*, Muri, on taro leaf in yard, 1♀, 24 March 1987 (JAB). Tupapa Valley, on grass, 1♂, 2 April 1987 (JAB). Taakoka Island, tree shaking, 1♂3♀6imm, 23 March 1987 (JWB & ERB). Arorangi, Are Metua at Rutaki Road, 1♂2imm, 9 March 1987 (JWB & ERB). Arorangi village, elev. 30 m, tree shaking, 1♂4imm, 14 March 1987 (JWB & ERB). Arorangi village, on house, 1♂, 9 March 1987 (JWB & ERB). Avarua, 0–100 m, 1♀5imm, August 1979 (N.L.H.Krauss) (BPBM). Avarua, 0–100 m, 3♂1imm, August 1979 (N.L.H.Krauss) (BPBM). Titikaveka, 0–100 m, 1♀imm, October 1977 (N.L.H.Krauss) (BPBM). *Aitutaki*, Tautu, tree shaking, 1♀2imm, 26 March 1987 (JAB & JWB). **AMERICAN SAMOA:** *Tutuila*, Fagatogo, shaken from dead lower leaves of bananas, 1♂3imm, 14 July 1973 (JAB). Fagatogo, shaken from dead lower leaves of bananas, 1♂2imm, 13 July 1973 (JAB). **FIJI:** *Viti Levu*, about 5 mi. W of Nausori, Nanduruloulou Res. Station, 1♂1♀2imm, 15 May 1980 (JAB). **SOCIETY ISLANDS:** *Moorea*, Paopao village, litter, elev. 100 m, 1♀2imm, 11 January 1987 (JWB & ERB). *Huahine*, Fare, 1♀2imm, February 1961 (N.L.H.Krauss) (BPBM). Fare, 0–100 m, 1♂, March 1972 (N.L.H.Krauss) (BPBM). *Raiatea*, Utotoa, 0–100 m, 1♀, March 1972 (N.L.H.Krauss). **MARQUESAS ISLANDS:** *Hiva Oa*, above Atuona, elev. 500 m, sweeping and shaking vegetation, 1♂3imm, 12 February 1987 (JWB & ERB). **AUSTRAL ISLANDS:** Rurutu, Moerai, 0–150 m, 1♂2♀1imm, October 1977 (N.L.H.Krauss) (BPBM). **GILBERT ISLANDS:** Pacific Sci. Bd., 1♂ (E.T. Moul) (BPBM).

**Distribution.**—Sumatra, New Hebrides, Fiji, Samoa, Marquesas, Hawaii, New Guinea,

Marianas, Ellice, Austral, Gilbert, Cook and Society Islands.

*Bavia sepxunctata* (Doleschall 1859)

Figs. 35–38, 46; Map 3

*Salticus sepxunctatus* Doleschall 1859.

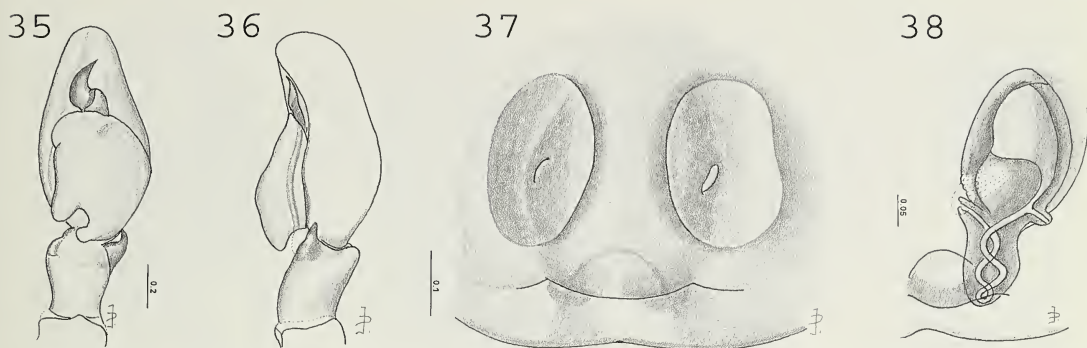
*Bavia sepxunctata*: Thorell 1890; Prószyński 1984; Żabka 1988.

*Acompsa dulcinervis* L. Koch 1879; Thorell 1881.

**Description.**—**Male:** ( $n = 5$ ). Total length 8.1–10.8 ( $\bar{x} = 9.14$ ), length of carapace 3.4–4.2 ( $\bar{x} = 3.74$ ), maximum carapace width 2.4–3.4 ( $\bar{x} = 2.96$ ), eye field length 1.8–2.2 ( $\bar{x} = 1.96$ ), eye row I width 2.0–2.5 ( $\bar{x} = 2.24$ ). Cephalothorax reddish-brown, gradually lighter dorsally, eye field dark brown, followed by broad transverse lighter area with a few whitish setae, a few small whitish scales along lateral eyes and a spot of white setae above junction of AME; posterior slopes of thorax and sides with few small erect black setae, sparse smaller brown ones, and a few irregular lines of white setae and scales. Abdomen with median area whitish limited by several pairs of elongate spots, lateral to which are many short narrow violet-brown spots, lower sides whitish, spinnerets light yellowish-brown. Face brown with white setae along ventral edge of clypeus, with triangular median patch of whitish setae above AME, and surrounded with inconspicuous reddish setae. ALE almost touching AME, diameter of AME = 2 diameters of ALE. Apical part of cymbium and prolateral part of its basal half whitish-yellow, retrolateral basal part brownish, tibia retrolaterally blackish, prolaterally whitish-yellow, patella and femur brown with marginal rows of short white setae. Seven retrolateral cheliceral teeth, three prolateral cheliceral teeth. Endites elongate with small triangular expansion pointed anteriorly. Endites, labium, anterior coxae and sternum brown, coxae II yellowish-brown, coxae III–IV whitish-yellow; abdomen ventrally greyish-white with light brown, sclerotized epigastric fold, long light grey rectangular area in the posterior third of abdomen, no dark ring around spinnerets. **Legs:** Leg formula 1-4-2-3; patella-tibia III shorter than IV. Patella-tibia I length 3.5–4.9 ( $\bar{x} = 4.02$ ). Inconspicuous spots of whitish setae prolaterally in middle patella and apical tibia. Tarsus I light yellow. **Palp:** With embolus broad and sickle-shaped, bulb with proximal bifurcation (Figs. 35, 36).

**Female:** ( $n = 5$ ). Total length 10.0–12.0 ( $\bar{x} = 11.04$ ), length of carapace 4.0–4.5 ( $\bar{x} =$





Figures 35–38.—*Bavia sexpunctata*. 35, Left palp ventrally; 36, Palp laterally; 37, Epigynum; 38, Internal structure of epigynum showing right spermatheca and ducts.

4.20), maximum carapace width 3.2–3.7 ( $\bar{x}$  = 3.32), eye field length 2.1–2.3 ( $\bar{x}$  = 2.20), eye row I width 2.3–2.5 ( $\bar{x}$  = 2.36). Behind eye field there is a light orange transverse area with fovea in the middle, with minute white setae; slopes of thorax and sides covered with sparse white setae. Face brown with line of longer, white setae along ventral edge of clypeus. Chelicerae bulging basally. Seven retrolateral cheliceral teeth, three prolateral cheliceral teeth. Pedipalps with flattened dorsal surfaces, yellow, medially dark brown, framed laterally with dense fringes of white, short setae. Endites elongate, externally rounded, without depressions or expansions. Chelicerae posteriorly, endites, labium, anterior coxae and sternum brown, coxae II yellowish-brown, coxae III–IV whitish yellow; abdomen ventrally greyish-white with light grey rectangular area in the posterior third of abdomen. A very small and inconspicuous protuberance with dark setae in front of spinnerets, no dark ring around spinnerets. *Legs*: Leg formula 1=4-2-3; patella-tibia III shorter than IV. Patella-tibia I length 3.4–3.8 ( $\bar{x}$  = 3.52). *Epigynum*: With large oval depressions separated by a septum much narrower than in *B. aeri-ceps*, internal ducts narrow (Figs. 37, 38).

**Material examined.**—CAROLINE ISLANDS: *Palau Islands*, Arakabesan I., mixed forest, shaken from trees, 50–75 ft. el., 1♂ 1imm, 16 February 1973, (JWB). Arakabesan I., in fallen betel palm fronds, 1♀ 6imm, 23 March 1973 (JWB & JAB). Malakal I., shaken from fallen palm fronds, 1♀ 4imm, 8 March 1973 (JWB & JAB). Koror I., shaken from trees at Japanese temple ruins, 1♀ 1imm, 17 March 1973 (JWB & JAB). Koror I., shaken from banana trees, 2♀ 1imm, 21 March 1973 (JAB & JWB). Koror I., taro patch, 2♂ 4♀ 17imm,

7 March 1973 (JAB & JWB). Koror I., near taro patch, from nipa palm inflorescences, 2♀, 9 May 1973 (JAB & JWB). Babelthuap I., Airai, low tropical forest N of airstrip, 2♂ 5♀ 14imm, 27 March 1973 (JAB & JWB). Babelthuap I., Airai, from fallen betel palm fronds, 2♀ 8imm, 11 March 1973 (JAB & JWB). Babelthuap I., Airai, tree shaking near SDA school, 1♂ 2♀, 11 March 1973 (JAB & JWB). Babelthuap I., Ngaremlengui, forest, 1♂ 9imm, 21 April 1973 (JAB & JWB). Peleliu I., mixed tropical forest, 2♀ 13imm, 22 March 1973 (JWB & ERB). Angaur I., shaken from trees, mixed tropical forest, 1♀ 3imm, 30 April 1973 (JAB & JWB). Angaur I., banana-betel palm community, 4♂ 2♀ 15imm, 27 April 1973 (JAB & JWB). Tobi I., shaken from trees, forest, 1♀ 23imm, 8 April 1973 (JWB & ERB). **MARSHALL ISLANDS**: *Kwajalein Atoll*, Ennylebegan, shaken from trees, 1♀, 21 July 1969 (JWB). *Kwajalein Atoll*, Gugeegu, shaken from trees, 1♀ 2imm, 24 July 1969 (JWB).

**Distribution.**—India to Australia, Caroline Islands, Marshall Islands.

*Bavia fedor* new species

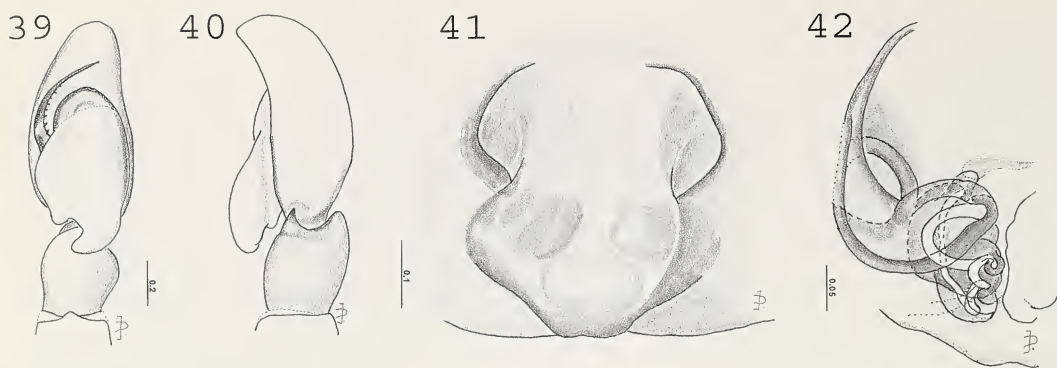
Figs. 39–42, 47; Map 3

**Holotype.**—Male from Caroline Islands, Yap, Yap Island, Fedor village, in taro patch, 11 February 1980 (J.W. Berry) (BPBM).

**Etymology.**—This species is named in honor of the people of Fedor village in the Yap Islands where it was collected.

**Diagnosis.**—Male with a distinct rounded dorsal tibial apophysis on the palp, in addition to the lateral apophysis; female epigynum with broad septum between openings (Fig. 41). Other species lack dorsal apophysis on male palp (Figs. 45–48) and have distinctly different epigyna.

**Description.**—*Male*: ( $n$  = 3). Total length



Figures 39–42.—*Bavia fedor* new species from Yap. 39, Left palp ventrally; 40, Palp laterally; 41, Epigynum; 42, Internal structure of epigynum showing left spermatheca and ducts.

6.0–7.5 ( $\bar{x}$  = 6.75), length of carapace 2.7–3.9 ( $\bar{x}$  = 3.26), maximum carapace width 2.0–3.0 ( $\bar{x}$  = 2.50), eye field length 1.3–1.9 ( $\bar{x}$  = 1.66), eye row I width 1.6–2.2 ( $\bar{x}$  = 1.90). Cephalothorax resembles *Bavia aericeps* except: face light brown with sparse greyish-brown setae, no contrasting line of white setae along ventral edge of clypeus, ALE aligned  $\frac{1}{4}$  of their diameter above dorsal rim of AME, almost touching them, diameter of AME = 2 diameters of ALE, pedipalps brownish-yellow, with a peculiar plate-like dorsal process on palpal tibia, apart from lateral apophysis, prominent but isolated bunches of longer greyish setae prolaterally on cymbium, tibia and patella. Endites elongate, broader apically and narrowing basally, with oval depression on the external apical edge followed by semi-circular expansion. Six retrolateral cheliceral teeth, three prolateral cheliceral teeth. *Legs*: Leg formula 1=4-2-3; patella-tibia III shorter than IV. Patella-tibia I length 2.2–4.1 ( $\bar{x}$  = 3.10). Leg I light brown with tarsus I whitish, inconspicuous spot of whitish setae prolaterally on patella; tarsus I white, remaining leg I brownish-yellow, denser and longer grey setae ventrally on patella-tibia-metatarsus I and along ventro-retrolateral edge of femur I; no such setae on legs II–IV, which are lighter, brownish-yellow. *Palp*: With bulb deeply notched proximally as in *B. sexpunctata*. Embolus long, slender and curved; attached near distal end of bulb.

*Female*: ( $n$  = 2). Total length 9.5–10.6 ( $\bar{x}$  = 10.05), length of carapace 3.8–4.6 ( $\bar{x}$  = 4.20), maximum carapace width 3.0–3.8 ( $\bar{x}$  = 3.40), eye field length 1.9–2.2 ( $\bar{x}$  = 2.05), eye row I width 2.2–2.4 ( $\bar{x}$  = 2.30). Six retrolateral

cheliceral teeth, four prolateral cheliceral teeth. *Legs*: Leg formula 1=4-2-3, patella-tibia III shorter than IV. Patella-tibia I length 3.1–3.9 ( $\bar{x}$  = 3.50). Coloration essentially as in male. *Epigynum*: See diagnosis and Figs. 41, 42).

**Material examined.**—CAROLINE ISLANDS:

Yap, Fedor Village, on coconut fronds, 1♀, 12 March 1980 (JWB). Fedor Village, taro patch, 1♂, 11 February 1980 (JWB). Fanif, on nipa palm petiole, 1♀, 14 April 1980 (JWB). Colonia, near house, 1♂, 19 March 1980 (JWB). Gagil-Tomil, shaking banana leaves, 1♀, 29 May 1973 (JAB & JWB). Fais Island, (no date), 1♀, E12087 (BPBM).

**Distribution.**—Known only from Yap and Fais in the Caroline Islands.

***Bavia sonsorol* new species**

Figs. 43, 44, 48; Map 3

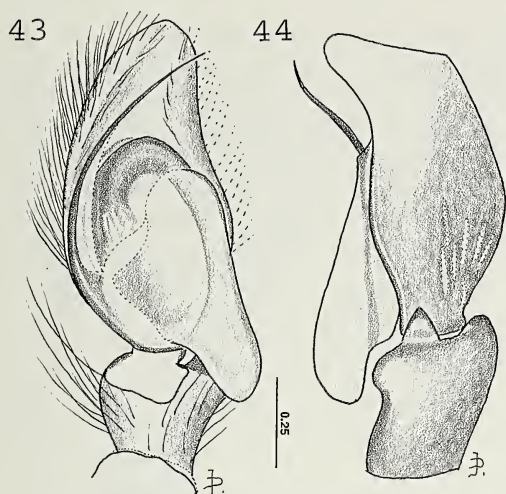
**Holotype.**—Male from Caroline Islands, Sonsorol Island, mixed tropical forest, 6 April 1973 (J.W. & E.R. Berry) (BPBM).

**Etymology.**—This species is named for the island of Sonsorol in the Palau Islands where it was collected.

**Diagnosis.**—Palp with broadly triangular lateral tibial apophysis which, in the only available specimen, is transparent and difficult to see. Lateral apophysis of the other species narrower basally (Figs. 43, 44, 45–48).

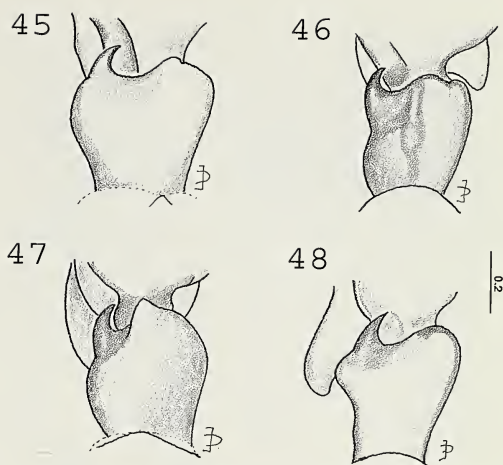
**Description.**—*Male*: ( $n$  = 1). Total length 8.1, length of carapace 3.5, maximum carapace width 3.2, eye field I length 1.6, eye row I width 1.9. Cephalothorax oval, broadening at the level of eyes III, brown, lighter dorsally, eye field fawn, followed by yellowish area behind, posterior slope of thorax dorsally lighter brown, yellowish at the hind margin. Cepha-





Figures 43, 44.—*Bavia sonsorol* new species from Sonsorol, Palau District. 43, Left palp ventrally (bulb collapsed); 44, Palp laterally.

lothorax almost bare, with whitish setae on thoracic slope and very dense whitish setae beneath and surrounding lateral eyes; a row of sparse short, indistinct setae diagonally from ALE along the crest of broadened area, somewhat reminiscent of cheeks in *Ascyltus*; a row of long colorless and yellowish horizontal setae above eyes I. Abdomen in alcohol whitish. Spinnerets yellowish-brown. Face light reddish-brown. Thick lines of white setae on the reddish-brown chelicerae: one vertical along prolateral edge, the second, transverse across basal part of chelicerae. ALE aligned  $\frac{1}{3}$  of their diameter above dorsal rim of AME, almost touching them, diameter of AME = 0.7, diameters of ALE = 0.3 mm. Endites elongate, semicircularly broader apically and narrowed basally, without oval depression on the external apical edge or any separate expansion. Chelicerae, endites, and labium brown, anterior coxae light brown, coxae II-IV whitish-yellow; sternum pale yellow, brown rimmed; abdomen ventrally greyish-white with light brown epigastric fold, light grey square area in the posterior part of abdomen, no dark ring around spinnerets. Five retrolateral cheliceral teeth, three prolateral cheliceral teeth. *Legs*: Leg formula presumably 1-4-2-3, but portions of the first legs missing. Patella-tibia III shorter than IV. Prolateral surface of femur I brown, shiny, its upper part and remaining parts of the segment with inconspicuous, sparse, short whitish setae. *Palp*:



Figures 45–48.—Comparison of left palpal tibia dorsally in four species of *Bavia*. 45, *Bavia aeri-ceps*; 46, *Bavia sexpunctata*; 47, *Bavia fedor* new species; 48, *Bavia sonsorol* new species.

Pedipalps light brown, almost bare, prolateral surface of palpal tibia broad, with anterior edge curved and rising dorsally; spots of white setae on dorsal half of patella and dorsally on cymbium, just in front of tibia, with triangular apophysis.

*Female*: Female is unknown.

**Material examined.**—Only the holotype.

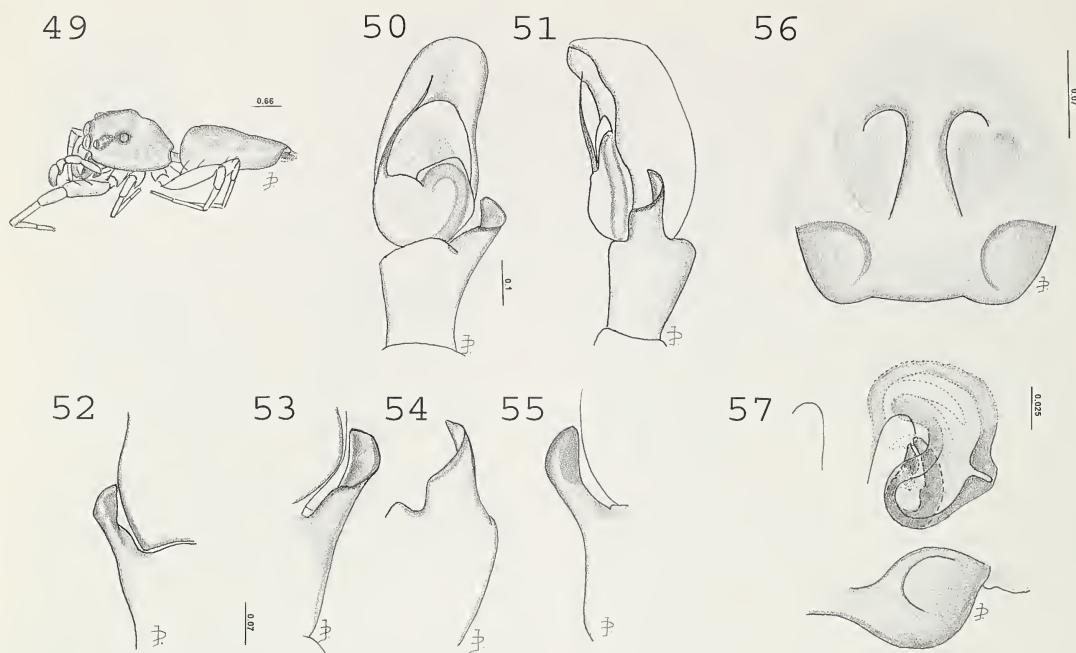
**Distribution.**—Known only from the island of Sonsorol in the Caroline Islands.

Genus *Cosmophasis* Simon 1901

**Discussion.**—Approximately 40 species are currently placed in this genus by Prószyński (1990), but he also states that the [nine] African species are not congeneric with those from Asia. No species of the genus have been reported previously from the Pacific Island region (as here defined). Bonnet (1956), quoted by Prószyński (1990), mistakenly listed *C. maculiventris* Strand 1911, from Indonesia, as occurring in Polynesia. Two species from New Guinea are illustrated by Chrysanthus (1968).

**Diagnosis.**—Medium-sized unidentate salticids of Simon's group Chrysilleae. Distinguished from other Pacific genera of the group by: ocular quadrangle parallel-sided or widening posteriad, long embolus and septate epigynum (Figs. 50, 56), and the covering of flattened iridescent scales over much of the body.

**Descriptive notes.**—Cephalothorax relatively low (42–50% of length of cephalotho-



Figures 49–57.—*Cosmophasis arborea* new species from Yap in the Caroline Islands. 49, General appearance of male; 50, Left palp ventrally; 51, Palp laterally; 52, Tibial apophysis dorsally; 53–55, Variation in tibial apophysis of another specimen —ventrally, laterally, and dorsally; 56, Epigynum; 57, Internal structure of epigynum, single spermatheca and ducts.

rax), with the highest point at the level of eyes III, from which it very gently slopes anteriorly and posteriorly to the posterior thoracic slope. When alive iridescent due to dense, minute scales which could be seen on preserved specimens only with difficulty. Abdomen elongate (with parallel sides in males, slightly more oval in females), gradually tapering posteri-

orly; spinnerets cylindrical and relatively long. Frontal aspect: eyes I aligned straight along dorsal-most point of their rim, ALE diameter  $\frac{1}{2}$ – $\frac{2}{3}$  of AME, clypeus very low, in some cases obsolete, chelicerae of average size, length about  $1\frac{1}{2}$  diameters of AME. Pedipalps slender. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. *Legs*: Thin and long, tibia I has two ventral rows of three spines each and two prolateral spines.

*Cosmophasis arborea* new species

Figs. 49–57; Map 4

**Holotype.**—Male from Yap, Yap Island, Colonia, litter and shaking trees on hill behind Protestant mission near bay, 31 May 1973 (J.W. Berry) (BPBM).

**Etymology.**—The name refers to the fact that many of the specimens were taken from trees.

**Discussion.**—The species is closely related to *Cosmophasis marxi* (Thorell 1890a) (Prószyński 1984:21–23) from Java. More distant relations include *Cosmophasis laticlavata* (Thorell 1892) from Sumatra, *Cosmophasis*



Map 4.—Distribution of three new species of *Cosmophasis* in the Pacific. *Cosmophasis arborea* new species (\*), *Cosmophasis lami* new species (□), and *Cosmophasis muralis* new species (Δ).



*olorina* (Simon 1901b) from Sri Lanka and the species from Java misidentified in the Simon collection as *C. "thalassina"*. All these species are relatives of the type species *C. thalassina* (C.L. Koch 1846) as redescribed by Żabka 1988, which differs by the anterior location of embolus, which arises from a broad basis, separated from the bulb, and by longer tibial apophysis.

**Diagnosis.**—Origin of embolus at about midlength of bulb prolaterally, shape of tibial apophysis and cymbium of male palp, and form of epigynum and its internal structure distinguish *arborea* from other Pacific species of the genus.

**Description.**—*Male:* ( $n = 5$ ). Total length 4.7–5.4 ( $\bar{x} = 5.10$ ), length of carapace 2.1–2.3 ( $\bar{x} = 2.21$ ), maximum carapace width 1.5–1.9 ( $\bar{x} = 1.75$ ), eye field length 1.0–1.7 ( $\bar{x} = 1.24$ ), eye row I width 1.3–1.5 ( $\bar{x} = 1.40$ ). Cephalothorax brown, eye field darker brown, lower rim of cephalothorax dark brown to almost black. Abdomen dark dorsally, with indistinct whitish, median lines and traces of 2–3 transverse lines; margins of dorsal surface with whitish rim, posterior tip of abdomen and spinnerets black. Minute dark bristles scattered over abdomen. Frontal aspect yellow, framed by dark brown eye field and blackish edge of clypeus; eyes I surrounded with white and yellowish scales; clypeus darker with a few large, colorless scales. Chelicerae fawn, near rectangular, apically depressed, with higher retrolateral and apical rim; the apical edge ends in a triangular tooth-like process, from that point the edge turns diagonally and is armed with two conical teeth, opposite fang's tip. Pedipalps slender, white with darker brown-yellow cymbium and prominent bent tibial apophysis. Palpal cymbium moderately elongate, with embolus arising anteriorly from a broad base, separated from bulb, tibial apophysis longer than related species, in form of a slightly twisted plate, with a diagonally cut tip; there is some variation in the shape of apophysis (Figs. 52–55). Ventral aspect: mouth parts light brown, sternum yellow with greyish-brown margin, coxae and ventral surfaces of femora yellowish-white; abdomen ventrally greyish-brown. *Legs:* Leg formula 1-4-3-2, patella-tibia III shorter than IV. Patella-tibia I length 2.1–2.6 ( $\bar{x} = 2.38$ ). Legs thin and long, yellow, legs I slightly darker

with grey spot laterally near extremities of tibia.

*Female:* ( $n = 3$ ). Total length 4.4–5.1 ( $\bar{x} = 4.85$ ), length of carapace 2.05–2.10 ( $\bar{x} = 2.07$ ), maximum carapace width 1.45–1.55 ( $\bar{x} = 1.50$ ), eye field length 1.05–1.10 ( $\bar{x} = 1.08$ ), eye row I width 1.1–1.4 ( $\bar{x} = 1.27$ ). Cephalothorax light brownish-yellow with slightly darker brown eye field; covered with adpressed scales, practically invisible, except on darker areas around eyes; lower rim of cephalothorax brown. Abdomen light brownish-yellow, with indistinct thin irregular lines of darker scales, one scale broad, along lateral margins, and three transverse lines; spinnerets greyish-yellow. Minute dark bristles scattered over abdomen. Frontal aspect yellow, framed dorsally by brown eye field; eyes I surrounded with white and yellowish scales; clypeus obsolete; with a triangle of longer scales between AME. Chelicerae yellow. Pedipalps white, with yellow tarsus. Ventral aspect whitish-yellow. *Legs:* Leg formula 4-1-3-2, patella-tibia III shorter than IV. Patella-tibia I length 1.3, 1.5 ( $n = 2$ ). Legs I thin and long, yellow. *Epigynum:* With two narrow grooves separated by a narrow rise, edges of plate rounded posteriorly (Figs. 56, 57).

**Material examined.**—CAROLINE ISLANDS: Yap, Colonia, night lighting, 1♀, 26 February 1980 (JWB). Colonia, litter and tree shaking on hills behind Evangelical Mission, 1♂, 31 May 1973 (JAB & JWB). Colonia, St. Mary's school, sweeping bushes, 1♀, 1 March 1980 (JWB). Dinay village, Pandanus/grass sweeping, 2♂ 1♀ 2imm, 4 March 1980 (JWB). Gitam, shrub shaking, 1♂, 8 April 1980 (JAB & JWB). Gilman, shaking mango tree, 1♂ 1imm, 15 April 1980 (JAB & JWB). Gagil-Tomil, shaking bananas, 2♂ 4imm, 2 May 1973 (JWB & JAB). Colonia, tower hill, shaking, 1♂ 5imm, 29 May 1973 (JWB & JAB). Map, Chool, tree shaking, 7♂ 2imm, 12 April 1980 (JWB & JAB).

**Distribution.**—Known only from Yap in the Caroline Islands.

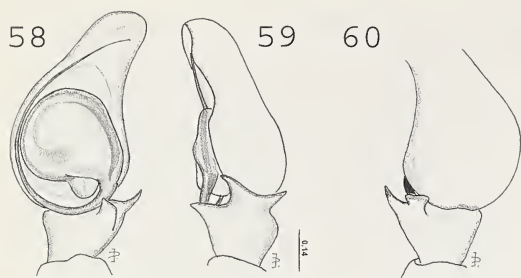
#### *Cosmophasis lami* new species

Figs. 58–60; Map 4

**Holotype.**—Male from Fiji, Viti Levu, Suva, Lami beach, on shrub foliage, 3 May 1987. (J.A. Beatty & E.R. Berry) (BPBM).

**Etymology.**—The specific name is a noun in apposition after the locality where the specimens were collected.

**Diagnosis.**—The long embolus originating



Figures 58–60.—*Cosmophasis lami* new species from Fiji. 58, Left palp ventrally; 59, Palp laterally; 60, Tibial apophysis dorsally.

at the retrolateral corner of the bulb and three-lobed palpal tibial apophysis distinguish *Cosmophasis lami* from males of other Pacific species.

**Description.**—*Male*: ( $n = 2$ ). Total length 5.3, 5.6; length of carapace 2.3, 2.3; maximum carapace width 1.5, 1.5; eye field length 1.1, 1.1; eye row I width 1.4, 1.5. Cephalothorax uniform orange except for dark eye field; covered with colorless to slightly brownish scales, except eye field which has dense orange setae, elongate scales above rims of eyes I whitish. Abdomen ventrally lighter with large colorless scales. Dorsal surface orange, with lighter yellow marginal line, in one specimen there are also two indistinct lines of brown scales just above marginal line, in the mid-length of abdomen; posterior tip of abdomen slightly darker, spinnerets blackish-grey. Minute dark bristles scattered over abdomen, almost invisible. Frontal aspect: yellowish-fawn; eyes I surrounded with whitish scales; clypeus appears bare but has minute sparse brown setae and bristles. Chelicerae orange, apically light

yellow. *Legs*: Leg formula 1-4-3-2, patella-tibia III shorter than IV. Patella-tibia I length 1.7, 1.7. Legs I deep yellow, other legs various shades of yellow. *Palp*: With rounded bulb, embolus arising at the five o'clock position and half-encircling bulb medially. Tibial apophysis with three triangular rami.

*Female*: Female is unknown.

**Material examined.**—**Fiji**: *Viti Levu*, Suva, Lami Beach, on shrub foliage, the holotype and 1 other ♂, 3 May 1987 (ERB & JAB).

**Distribution.**—Known only from Viti Levu, Fiji.

*Cosmophasis muralis* new species

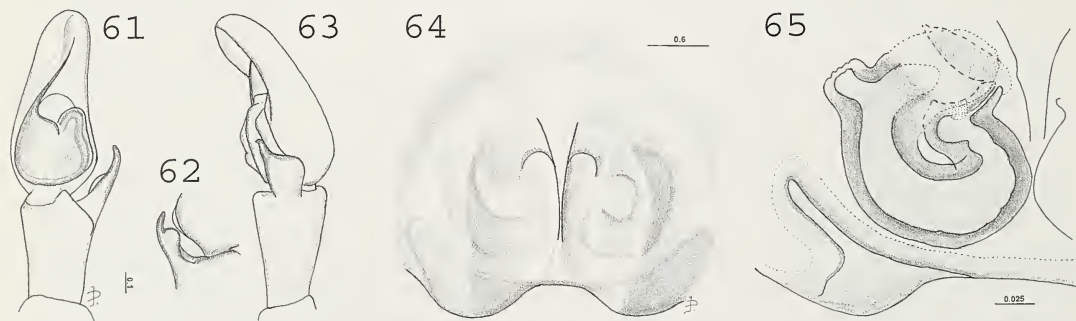
Figs. 61–65; Map 4

**Holotype.**—Male from Koror, Palau, on lab building, 8 March 1973 (J.A. Beatty & J.W. Berry) (BPBM).

**Etymology.**—*Muralis*, of the walls, because several specimens were collected on the outer walls of buildings.

**Diagnosis.**—The nearly straight embolus, about half the length of the cymbium, arising from anterior margin of the bulb, shape of male palpal tibial apophysis (resembling that of *Cosmophasis chlorophthalma* (Simon 1898)) and form of the epigynum and its outer ducts separate *C. muralis* from the other Pacific species of the genus.

**Description.**—*Male*: ( $n = 5$ ). Total length 6.1–7.7 ( $\bar{x} = 6.86$ ), length of carapace 2.5–3.2 ( $\bar{x} = 2.82$ ), maximum carapace width 1.9–2.3 ( $\bar{x} = 2.01$ ), eye field length 1.2–1.4 ( $\bar{x} = 1.30$ ), eye row I width 1.6–1.9 ( $\bar{x} = 1.69$ ). Cephalothorax brown with a transverse line of whitish scales behind eye field, eye field darker brown with colorless broad scales; ven-



Figures 61–65.—*Cosmophasis muralis* new species from Palau in the Caroline Islands. 61, Left palp ventrally; 62, Tibial apophysis dorsally; 63, Palp laterally; 64, Epigynum; 65, Internal structure of epigynum—single spermatheca and ducts.



tral margin with streak of whitish scales, bending on face and coming to the sides of AME. Abdomen reddish-brown with thin median whitish streak, and white margin around  $\frac{3}{4}$  of abdomen, ending by small triangular spot; spinnerets darker. Frontal aspect: a row of horizontal bristles above eyes I, which are also surrounded dorsally by dense row of yellowish, inconspicuous setae, laterally and ventrally by whitish setae, clypeus yellowish-fawn, almost bare; chelicerae longer than usual, brown, with anterior surface flattened and apically depressed and limited by apical sclerotized ridge. *Legs*: Relative leg length 1.4–2=3, with patella-tibia III shorter than IV. Patella-tibia I length 2.3–3.2 ( $\bar{x}$  = 2.59). Legs light yellow, legs I with darkened prolateral surfaces of femur, tibia and metatarsus. *Palp*: Whitish, slender (see diagnosis and Figs. 61–63).

*Female*: ( $n$  = 5). Total length 6.3–7.1 ( $\bar{x}$  = 6.79), length of carapace 2.6–2.9 ( $\bar{x}$  = 2.74), maximum carapace width 1.8–2.1 ( $\bar{x}$  = 1.98), eye field length 1.3–1.4 ( $\bar{x}$  = 1.30), eye row I width 1.6–1.7 ( $\bar{x}$  = 1.67). Differs from male by lack of white line behind eye field, marginal white belt developed but indistinct on the background of yellowish lower sides; abdomen with two transverse white lines in the posterior half, anterior half bisected by thin median line and with thin white margin. *Legs*: Leg formula 4-3-1-2, patella-tibia III shorter than IV. Patella-tibia I length 1.7–1.9 ( $\bar{x}$  = 1.83). *Epigynum*: With narrow septum and two broad lunate posterior lobes.

#### Material examined.—CAROLINE ISLANDS:

*Palau*, Koror, on entomology lab building, 1♂ (holotype) 1♀ imm, 8 March 1973 (JAB & JWB). *Koror*, entomology lab on outside building wall, 1♂, 7 March 1973 (JAB). *Koror*, entomology laboratory building, 2♂4imm, 24 February 1973 (JWB & JAB). *Koror*, taro patch, 1♀4imm, 7 March 1973 (JWB). *Koror*, Japanese temple ruins, tree shaking, 1♀, 17 March 1973 (JAB & JWB). *Koror*, in cave entrance, 1♀, 17 March 1973 (JWB & JAB). *Koror*, scrub forest in vacant lot, tree shaking, 1♀, 13 February 1973 (JWB & JAB). *Koror*, entomology lab building, 1♂, 25 March 1973 (JWB & JAB). *Koror*, scrub forest in a vacant lot, tree shaking, 1♂2imm, 14 May 1973 (JAB). *Babelthuap*, Ngaremlengui, in woods, 1♂1♀ imm, 21 April 1973 (JWB & JWB). *Angaur*, banana-betel palm, 2♂, 27 April 1973 (JWB & JAB). *Peleliu*, mixed tropical forest, 3♂2♀16imm, 22 March 1973 (JWB & ERB).

**Distribution.**—Known only from the Palau group of the Caroline Islands.

Genus *Flacillula* Strand 1932  
(*Flacilla* Simon 1901 —preoccupied)

**Discussion.**—The genus contains at present four species described from the Oriental Region and Pacific Islands. Palpal organs of the specimens studied correspond to that of the type species *Flacillula lubrica* (Simon 1901) (cf. Prószyński 1984:77) from Sri Lanka, general features of the epigynum agree with that of *Flacillula incognita* Žabka 1985 from Vietnam. *Flacilla kraussi* Marples 1964 has the typical stridulating apparatus of *Pseudicius* Simon 1885 and is here transferred to that genus (NEW COMBINATION).

**Diagnosis.**—Small, elongate unidentate salticids with all legs completely spineless except for one small distal prolateral spine on metatarsus I in both sexes. First legs robust with distal segments very short (tibia length = patella; metatarsus and tarsus shorter).

**Descriptive notes.**—Minute jumping spiders with shiny cephalothorax. The body is low and narrow. Abdomen elongate oval, 25–38% longer than cephalothorax, as broad as cephalothorax; in males covered by scutum, in females covered by thin tegument, with grey pigmented pattern. Face very low, its whole height occupied by AME, clypeus obsolete, diameter of ALE  $\frac{2}{3}$  of AME, eyes I aligned in a straight line by their dorsal rims. Legs I are robust in both sexes, much broader than the others, with tibia and patella block-like with prominent angles; in male legs I are the longest, while in female the longest are IV (115–120%), legs II and III are practically of the same length in both sexes. The palpal organ is very simple; epigynum, also rather simple, so small that details are visible only with a compound microscope.

*Flacillula minuta* (Berland 1929)

Figs. 66–68, 71–74; Map 5

*Flacilla minuta* Berland 1929a.

*Flacillula minuta* (Berland): Strand 1932.

**Holotype.**—Female from Samoa, Upolu, Malololelei, 2000 ft., (Buxton & Hopkins, in BMNH, examined).

**Description.**—*Male*: ( $n$  = 5). Total length 2.7–2.8 ( $\bar{x}$  = 2.70), length of carapace 1.05–1.4 ( $\bar{x}$  = 1.24), maximum carapace width 0.7–0.9 ( $\bar{x}$  = 0.81), eye field length 0.55–0.60 ( $\bar{x}$

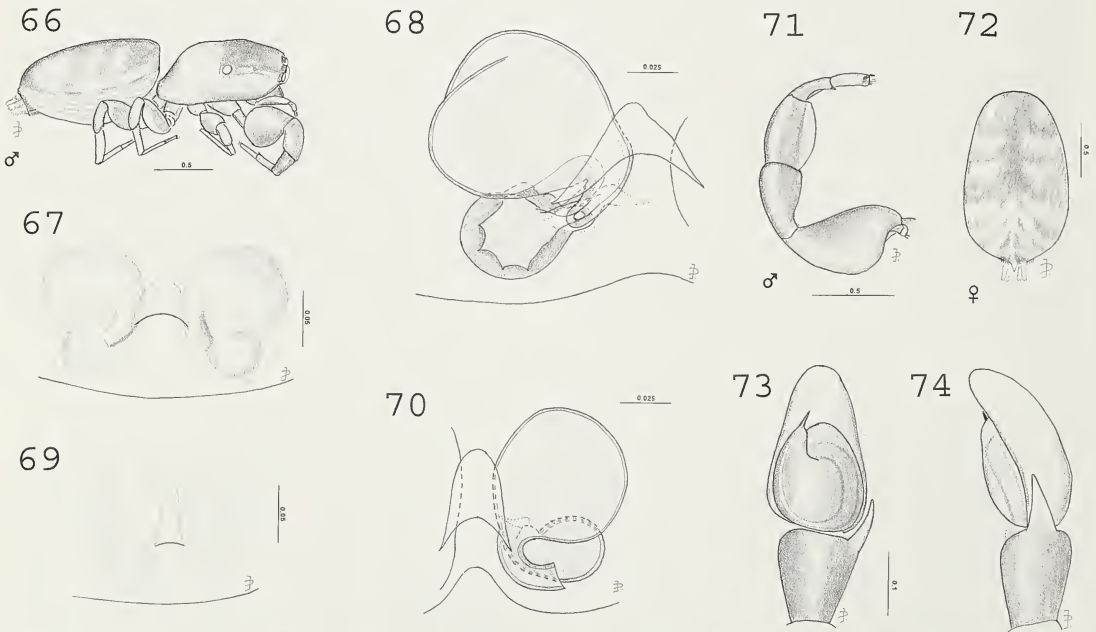


Map 5.—Distribution of two species of *Flacillula* in the Pacific. *Flacillula minuta* (■), *Flacillula nitens* new species (□).

= 0.59), eye row I width 0.6–0.7 ( $\bar{x}$  = 0.68). Cephalothorax shiny brown, with eye field darker, covered with minute papillae, and lines of similar papillae radiating from the fovea over the thorax and sides. Microscopic colorless setae scattered over eye field. Abdomen with distinct shiny brown scutum, integument

with pattern consisting of median grey area with lateral branches, but sometimes merging into larger grey areas. One retrolateral cheliceral tooth, three prolateral cheliceral teeth, of which two are very small. *Legs*: Leg formula 1-4-2-3; patella-tibia III shorter than IV. Patella-tibia I length 0.7–0.95 ( $\bar{x}$  = 0.85). Legs I light brown, remaining legs yellow; width of tibia I 54% of femur I, 61% of the length of respective segment. *Palp*: Embolus very thin and short, apical on bulb (Figs. 73, 74).

*Female*: ( $n$  = 5). Total length 2.8–3.15 ( $\bar{x}$  = 3.01), length of carapace 1.15–1.30 ( $\bar{x}$  = 1.24), maximum carapace width 0.8–0.9 ( $\bar{x}$  = 0.86), eye field length 1.15–1.30 ( $\bar{x}$  = 1.24), eye row I width 0.7–0.75 ( $\bar{x}$  = 0.72). Cephalothorax with more setae than male. Abdomen similar to male. One retrolateral cheliceral tooth, three prolateral cheliceral teeth. *Legs*: Leg formula 4-1-3-2; patella-tibia III shorter than IV. Patella-tibia I length 0.65–0.70 ( $\bar{x}$  = 0.68). Leg color as in male; width of tibia I 57% of femur I, 67% of the length of respective segment. *Epigynum*: With wide central hood (Figs. 67, 68).



Figures 66–74.—The genus *Flacillula*. 66–68, *Flacillula minuta*. 66, General appearance of male; 67, Epigynum; 68, Internal structure of epigynum —single spermatheca and ducts; 69, 70, *Flacillula nitens* new species from Ponape. 69, Epigynum; 70, Internal structure of epigynum —single spermatheca and ducts. 71–74, *Flacillula minuta*. 71, Leg I of male, prolaterally; 72, Abdominal pattern of female; 73, Left palp ventrally; 74, Palp laterally.



**Material examined.**—**COOK ISLANDS:** *Rarotonga*, Muri, shaking trees in yard, 1♂1♀1imm, 25 March 1987 (JWB & JAB). Turangi Valley, shaking trees, elev. 20 m, 1♂, 1 April 1987 (JWB & ERB). Turangi stream valley, near Ngatangia, shaking trees, 1♂1♀3imm, 18 March 1987 (JWB, ERB & JAB). Oneroa Island, sweeping, 1♀, 21 March 1987 (JWB & ERB). Arorangi Village, on citrus trees, 2♀4imm, 18 March 1987 (JWB & ERB). Taakoka Island, shaking trees, 3♀2imm, 23 March 1987 (JWB & ERB). **CAROLINE ISLANDS:** *Truk*, Moen, coconut trash, 1♂, 12 June 1973 (JWB & JAB).

**Distribution.**—Known from Caroline Islands, Niue, Samoa, and Cook Islands.

*Flacillula nitens* new species

Figs. 69, 70; Map 5

**Holotype.**—Female from Ponape, mountain top, tree shaking, 6 June 1973 (J.W. Berry & J.A. Beatty) (BPBM).

**Etymology.**—The name *nitens*, shining, refers to the shiny cuticle of the spider.

**Diagnosis.**—Epigynum narrower than in *Flacillula minuta* (Figs. 67, 69).

**Description.**—*Female:* ( $n = 2$ ). Total length 2.75, 2.80, length of carapace 1.1, 1.1, maximum carapace width 0.7, 0.7, eye field I length 0.50, 0.55, eye row I width 0.6, 0.6. Differs from *Flacillula minuta* (Fig. 72) by having bare, shiny cephalothorax, abdomen in one specimen is bare and shiny, on second specimen there is grey pigmentation consisting of dense, irregular grey spots on light background. One retrolateral cheliceral tooth, three prolateral cheliceral teeth. *Legs:* Relative leg length 4-1=2=3; patella-tibia III shorter than IV. Patella-tibia I length 0.55 ( $\bar{x} = 0.55$ ). *Epigynum:* With narrow hood (Fig. 69).

*Male:* The male is unknown.

**Material examined.**—**CAROLINE ISLANDS:** *Ponape*, mountain top, tree shaking, 1♀, 6 June 1973 (JWB & JAB). East of Kolonia, breadfruit/ivory nut forest, hand collecting, 1♀1imm, 8 June 1973 (JWB & JAB).

**Distribution.**—Known only from Ponape in the Caroline Islands.

Genus *Frigga* C.L. Koch

**Diagnosis.**—Medium-to-large unidentate salticids distinguished by Galiano (1979) in her revision of the genus by the presence of a bifid apophysis on the male palp and a deep notch, in which lies a scape, in the posterior

margin of the epigynum. A South American genus apparently introduced in the Pacific.

*Frigga crocuta* (Taczanowski 1878)

*Amycus crocutus* Tacz. 1878

*Sandalodes calvus* Simon 1902

*Phiale bispinosa* Banks 1930

*Frigga crocuta* (Tacz.): Galiano 1979

**Discussion.**—This species was formerly included in the genus *Sandalodes* Keyserling 1883 as *S. calvus* Simon 1902 and is apparently of South American origin (Galiano 1979). It occurs across the Pacific from South America to Australia. We have collected it only from the eastern Pacific islands, and it is especially common in the Marquesas Islands. It has been illustrated recently by Davies & Žabka (1989). The other eight species of the genus are restricted to South America (Galiano 1979).

**Measurements.**—*Male:* ( $n = 5$ ). Total length 6.4–9.2 ( $\bar{x} = 7.76$ ), length of carapace 3.2–4.6 ( $\bar{x} = 3.78$ ), maximum carapace width 2.3–3.5 ( $\bar{x} = 2.84$ ), eye field length 1.4–1.8 ( $\bar{x} = 1.54$ ), eye row I width 1.8–2.3 ( $\bar{x} = 2.02$ ). One retrolateral cheliceral tooth, two prolateral cheliceral teeth (sometimes low and set very close together, appearing to be a single notched tooth). *Legs:* Leg formula 1-3=4-2; patella-tibia III equal to IV. Patella-tibia I length 3.2–5.5 ( $\bar{x} = 4.14$ ).

*Female:* ( $n = 5$ ). Total length 6.2–7.6 ( $\bar{x} = 6.92$ ), length of carapace 2.8–3.2 ( $\bar{x} = 3.02$ ), maximum carapace width 1.9–2.4 ( $\bar{x} = 2.20$ ), eye field length 1.2–1.4 ( $\bar{x} = 1.26$ ), eye row I width 1.6–1.8 ( $\bar{x} = 1.74$ ). One retrolateral cheliceral tooth, two prolateral cheliceral teeth. *Legs:* Leg formula 4-3-1-2; patella-tibia III=IV. Patella-tibia I length 1.7–2.0 ( $\bar{x} = 1.92$ ).

**Material examined.**—**MARQUESAS ISLANDS:** *Nuku Hiva*, Taiohae, grassy knoll, elev. 200 m, 2♂2♀20imm, 21 January 1987 (JWB & ERB). Taiohae, Governor's residence, shaking dead shrubbery, 1♂9imm, 21 January 1987 (JWB & ERB). Taiohae, trash pile in culvert, 1♂2♀3imm, 21 January 1987 (JWB & ERB). Taiohae, sweeping bushes, 1♂1♀5imm, 22 January 1987 (JWB & ERB). Taiohae, tree shaking, open field, 5♂16imm, 22 January 1987 (JWB & ERB). Taiohae, hibiscus litter, 1♂3imm, 22 January 1987 (JWB & ERB). Taiohae, sweeping, elev. 800 m, 5imm, 23 January 1987 (JWB & ERB). Taiohae, on buildings, 4imm, 25 January 1987 (JWB & ERB). Taipivai valley, tree shaking, 1♀5imm, 27 January 1987 (JWB &

ERB). Toovii, tree shaking, 600 m, 1♂2♀13imm, 27 January 1987 (JWB & ERB). Toovii, tree shaking, 600 m, 1♀6imm, 28 January 1987 (JWB & ERB). Cove west of Taiohae, litter near sea, 1♀, 30 January 1987 (JWB & ERB). Airport, almost desert conditions, sweeping low vegetation, 2♂4♀24imm, 14 February 1987 (JWB & ERB). *Hiva Oa*, Hanamenu, tree shaking, 1♂3♀23imm, 4 February 1987 (JWB & ERB). Hanamenu, top of E ridge, 1♂3♀8imm, 5 February 1987 (JWB & ERB). Hanamenu, in grass clump, 1imm, 6 February 1987 (JWB & ERB). Atuona, shaking low vegetation, 2♂10imm, 8 February 1987 (JWB & ERB). Atuona, roadside vegetation, 1imm, 9 February 1987 (JWB & ERB). Atuona, coconut/philodendron, sweeping and shaking, 1♂1imm, 10 February 1987 (JWB & ERB). Atuona, shaking roadside vegetation, 1imm, 10 February 1987 (JWB & ERB). Atuona, roadside sweeping, 5imm, 11 February 1987 (JWB & ERB). *Fatu Hiva*, Hanavave, coconut forest, sweeping & shaking, 1♀, 13 February 1987 (JWB & ERB). *Ua Pou Is.*, Hakahatau Airport, 100 m, 2♀, 12 July 1988 (S.L. Montgomery) (BPBM). Nuku Hiva, Terre Deserte, Ha'atuatua V, 1♂, 2 July 1988 (S.L. Montgomery) (BPBM). **TUAMOTU ISLANDS:** *Rangiroa Is.*, Avatoru, swept at light, 1♀, 28 August 1988 (S.L. Montgomery) (BPBM). **SOCIETY ISL.:** *Huahine*, Fare, 0–100 m, 1♂, March 1979 (N.L.H. Krauss) (BPBM). *Huahine*, Fare, 0–100 m, 1♂, March 1972 (N.L.H. Krauss) (BPBM). *Moorea*, Paopao, sweeping grass, 3 imm, 11 January 1987 (JWB & ERB). *Tahiti*, Tautira, 2♀, January 1961 (N.L.H. Krauss) (BPBM). *Raiatea*, Uturoa, 1♀, February 1961 (N.L.H. Krauss) (BPBM). **NEW CALEDONIA:** *Col de la Pirogue*, 1♀, 14 February 1963 (Yoshimoto) (BPBM). **COOK ISLANDS:** *Rarotonga*, Arorangi reservoir, roadside sweeping, elev. 50 m, 2imm, 1 March 1987 (JWB & ERB). Arorangi village, grass litter, 1imm, 4 March 1987 (JWB & ERB). Arorangi village, tree shaking, 1imm, 11 March 1987 (JWB & ERB). Arorangi village, tree shaking, elev. 30 m, 1♂2♀4imm, 14 March 1987 (JWB, ERB & JAB). Arorangi village, tree shaking, near Raemaru, elev. 250 m, 1imm, 14 March 1987 (JWB, ERB & JAB). Turangi village, tree shaking, elev. 100 m, 1♀1imm, 1 April 1987 (JWB, ERB & JAB). Inland from Muri Beach, tree shaking, elev. 20 m, 1imm, 4 March 1987 (JWB & ERB). Rutaki Road, tree shaking, 1♂1imm, 4 March 1987 (JWB & ERB). Tuoro hill, elev. 200 m, tree shaking, 4♂3imm, 10 March 1987 (JWB & ERB). Matavera, 0–100 m, 1♀, March 1976 (N.L.H. Krauss) (BPBM). Avarua, 0–100 m, 1♂3♀3imm, February 1979 (N.L.H. Krauss) (BPBM). Avarua, 0–100 m, 1♀, December 1977 (N.L.H. Krauss) (BPBM). Avarua valley, 0–150 m, 2♀, November 1977 (N.L.H. Krauss) (BPBM).

**Distribution.**—South America, Australia, New Caledonia and the Cook, Galapagos, Mangareva, Marquesas, Society and Tuamotu Islands.

#### Genus *Ligurra* Simon 1903

**Diagnosis.**—Small fissidentate salticids with sternum narrow anteriorly and first coxae close together. General appearance short, broad and short-legged, similar to *Rhene* Thorell 1869 and *Stertinus* Simon 1890. Differs from *Rhene* by having simpler genitalia in both sexes, from *Stertinus* by having third eye row not at posterior edge of flat part of carapace, by lacking lateral spines on metatarsus I, and retrolateral cheliceral tooth bicuspid rather than tricuspid. The latter character may be unreliable. Only one other species is placed in the genus at present (see diagnosis of the new species below).

**Descriptive notes.**—Fissidentate, with bicuspid tooth. Male chelicerae concave with a ridge edging the concavity; fang with two anterior spurs which close to either side of a distal flap on the paturon; female chelicerae normal, no spurs, flap or concavity.

#### *Ligurra opelli* new species

Figs. 75–80

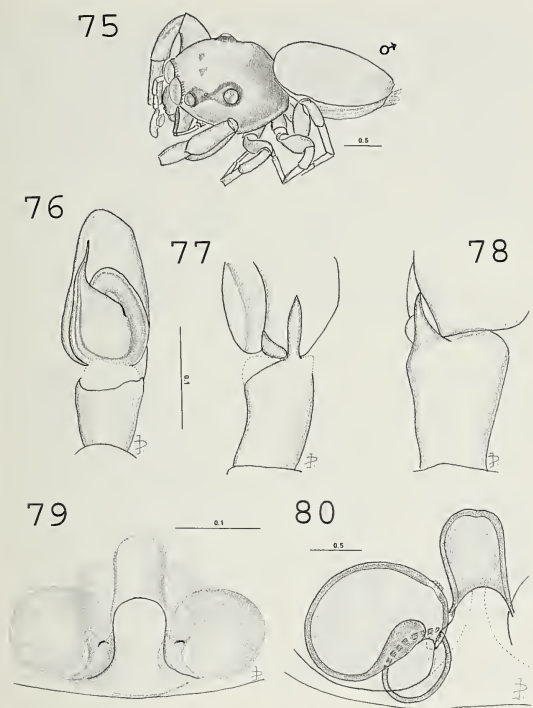
**Holotype.**—Male, mixed tropical forest, woods below SDA school, Airai, Babelthup, Palau, Caroline Islands, 11 March 1973 (Berry, Berry & Beatty) (BPBM).

**Etymology.**—This species is named for Dr. Brent Opell, an arachnologist at Virginia Polytechnic Institute and State University at Blacksburg, Virginia.

**Diagnosis.**—Male with embolus tapering, but almost straight, that of *L. latidens* (Dolleschall 1859) is distinctly curved. Tibial apophysis of palp slender and straight. Female with epigynal openings located near a narrow median hood. The female of *L. latidens* has no hood and the openings are at the posterior edge of the epigynum (Figs. 75–80).

**Description.**—*Male:* ( $n = 5$ ). Total length 2.9–3.3 ( $\bar{x} = 3.13$ ), length of carapace 1.3–1.7 ( $\bar{x} = 1.52$ ), maximum carapace width 1.3–1.5 ( $\bar{x} = 1.46$ ), eye field length 0.9–1.1 ( $\bar{x} = 0.96$ ), eye row I width 1.1–1.3 ( $\bar{x} = 1.23$ ). Stocky build, flattened, with abdomen overhanging sloping part of the thorax. Cephalothorax yellowish-brown, covered with sparse, whitish setae, ventral edge dark brown and





Figures 75–80.—*Ligurra opelli* new species from Caroline Islands. 75, General appearance of male; 76, Left palp ventrally; 77, Palp laterally; 78, Tibial apophysis dorsally; 79, Epigynum; 80, Internal structure of epigynum showing single spermatheca and ducts.

bare, with a narrow line of short white setae above. Lateral eyes narrowly surrounded with black pigmentation, eyes II in the middle between ALE and III. Abdomen yellowish-brown with indistinct pattern of lighter spots; the entire dorsum covered by scutum. Face low and broad, eyes I in a straight line, ALE separated from AME by about half their diameter, which diameter is half that of AME, clypeus reduced, light brown with a thin line of white setae under ALE only. Setae encircling dorsal rims of eyes I are white in male, contrasting with darker clypeus. Chelicerae short and broad, anteriorly concave, with retrolateral edge sclerotized; cheliceral fang with two anterior triangular protuberances and corresponding flap on prolateral edge of chelicera near fang: these are developed to different degrees in males of the same sample—from prominent to nearly invisible. One retrolateral cheliceral tooth, three prolateral cheliceral teeth. Ventral aspect: light brown to yellow, with abdomen lighter. *Legs*: Leg formula

1-4-2-3; legs I distinctly longer than others. Legs short, the first very robust, II–IV less so. Patella-tibia I length 1.1–1.7 ( $\bar{x}$  = 1.44) with patella-tibia III shorter than IV. *Palp*: See diagnosis and Figs. 76–78.

*Female*: ( $n$  = 5). Total length 3.6–4.7 ( $\bar{x}$  = 3.92), length of carapace 1.6–1.8 ( $\bar{x}$  = 1.69), maximum carapace width 1.5–1.7 ( $\bar{x}$  = 1.58), eye field length 0.9–1.1 ( $\bar{x}$  = 1.06), eye row I width 1.3–1.4 ( $\bar{x}$  = 1.35). Setae encircling dorsal rims of eyes I are colorless in female; also, entire clypeus covered with long white setae. Abdomen, except for the margins, covered by scutum. One bicuspid retrolateral cheliceral tooth, three prolateral cheliceral teeth. *Legs*: Leg formula 1 $\equiv$ 4-2-3; patella-tibia III shorter than IV. Patella-tibia I length 1.1–1.5 ( $\bar{x}$  = 1.26). *Epigynum*: See diagnosis and Figs. 79, 80.

**Material examined.**—**CAROLINE ISLANDS:** *Palau Islands*, Kayangel Atoll, coconut/*Barringtonia*, tree shaking, 2♂2♀, 22 May 1973 (JWB). Kayangel Atoll, in cycad tree, 1♂, 22 May 1973 (JWB). Koror, scrub forest in vacant lot, tree shaking, 5♂3♀10imm, 13 March 1973 (JWB & JAB). Koror, scrub forest in vacant lot, tree shaking, 3♂2♀19imm, 13 February 1973 (JWB). Peleliu, tree shaking, *Casuarina* forest, 1♂7imm, 21 March 1973 (JWB & ERB). Pulo Anna, tree shaking, coconut/shrub, 1♂, 7 April 1973 (JWB & ERB). Son-sorol, mixed tropical forest, 1♀7imm, 6 April 1973 (JWB & ERB). Arakabesan, mixed tropical forest, elev. 50–75 ft., tree shaking, 1♂4imm, 16 February 1973 (JWB & ERB). Babelthup, Airai, woods below SDA school, mixed tropical forest, tree shaking, 1♂, 11 March 1973 (JAB & JWB). Malakal, dry tropical forest, tree shaking, 1♀, 14 March 1973 (JWB, ERB & JAB). *Ponape*, Kolonia, on building, 1♀, 28 March 1980 (JAB).

**Distribution.**—Known from the Caroline Islands: Palau District and Ponape.

Genus *Plexippus* C.L. Koch 1846

**Diagnosis.**—A medium-to-large cosmopolitan unidentate genus belonging to Simon's Plexippeae. Prószyński (1990) lists 56 species in the genus. Differs from other genera of that group by having two whorls of spines (rather than three) on metatarsus III, by the broad angular bulb of the male palp and the epigynal structure, which lacks the large “windows” and narrow septum of *Palpelius* Simon 1903 (figs. 109, 112). One retrolateral cheliceral tooth, two prolateral cheliceral teeth.



Map 6.—Overlapping distribution of two species of *Plexippus* in the Pacific. *Plexippus paykullii* ( $\Delta$ ), a widely distributed pantropical species, and *Plexippus petersii* ( $\blacktriangle$ ), which is also known from India and Mozambique.

*Plexippus paykullii* (Audouin 1825)

Map 6

*Attus paykullii* Aud. 1825

*Plexippus paykulli* (Aud.): Paesi 1883

*Apamamia bocki* Roewer 1944 NEW SYNONYMY

**Discussion.**—This widespread cosmopolitan species is synanthropic and is considered as a “tramp” species. It has been illustrated many times, recently by Prószyński (1987) and Žabka (1990). Bonnet (1958) lists numerous other synonyms.

**Measurements.**—*Male*: ( $n = 5$ ). Total length 7.5–8.9 ( $\bar{x} = 8.46$ ), length of carapace 3.5–4.5 ( $\bar{x} = 4.09$ ), maximum carapace width 2.9–3.2 ( $\bar{x} = 3.08$ ), eye field length 1.7–1.9 ( $\bar{x} = 1.82$ ), eye row I width 2.2–2.5 ( $\bar{x} = 2.35$ ). *Legs*: Leg formula 4-1-3-2; patella-tibia III shorter than IV. Patella-tibia I length 3.6–4.3 ( $\bar{x} = 4.00$ ).

*Female*: ( $n = 5$ ). Total length 8.1–10.1 ( $\bar{x} = 9.14$ ), length of carapace 3.4–4.3 ( $\bar{x} = 3.84$ ), maximum carapace width 2.5–3.1 ( $\bar{x} = 2.76$ ), eye field length 1.6–1.8 ( $\bar{x} = 1.75$ ), eye row I width 2.1–2.5 ( $\bar{x} = 2.23$ ). *Legs*: Leg formula 4-3-1-2; patella-tibia III equal to IV. Patella-tibia I length 2.5–3.1 ( $\bar{x} = 2.76$ ).

**Material examined.**—**MARSHALL ISLANDS**: *Eniwetok*, 5♂20♀30imm (JWB & JAB). **HAWAII**: *Midway Is.*, 1♂2♀5imm (J. Richardson). **MALAYSIA**: *Penang*, 1♂ (JAB). **MARQUESAS ISLANDS**: *Nuku Hiva*, 4♂7♀12imm (JWB & ERB). *Hiva Oa*, 1imm (JWB & ERB). **FIJI**: *Viti Levu*, 2♂1♀ (JAB, JWB & ERB). **SOCIETY ISLANDS**: *Moorea*, 1♂ (JWB & ERB). **TUAMOTU ISLANDS**: *Manihi*, 5♀5imm (ERB).

**Distribution.**—Pantropical species, widely

distributed; cosmopolitan in warm climates, overlaps distribution of *Plexippus petersi* on some islands. N & S America (Mexico, SE USA: to Texas); Mediterranean (including Israel), S Europe, Africa, S & E Asia, Australia, Oceania.

*Plexippus petersii* (Karsch 1878)

Map 6

*Euophrys petersii* Karsch 1878

*Plexippus petersi* (Karsch): Simon 1903

**Discussion.**—This species, less common than *Plexippus paykullii*, overlaps the distribution of that species in Fiji and in Majuro (Marshall Islands). However, *P. paykullii*, although often taken on buildings, is frequently found associated with forests or other vegetation, while *P. petersii* is more strictly limited to buildings. Almost all of the specimens reported here were found associated with buildings (except for those from uninhabited Helen Reef). Illustrated by Žabka (1985) and Prószyński (1987).

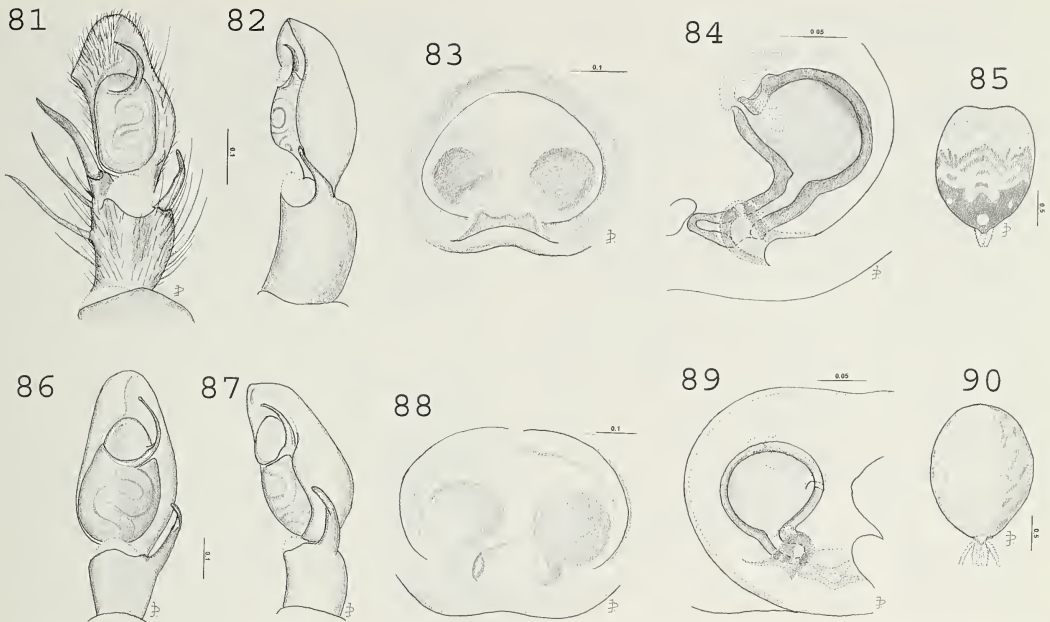
**Measurements.**—*Male*: ( $n = 5$ ). Total length 5.6–7.3 ( $\bar{x} = 6.34$ ), length of carapace 2.9–3.5 ( $\bar{x} = 3.14$ ), maximum carapace width 2.0–2.7 ( $\bar{x} = 2.40$ ), eye field length 1.3–1.6 ( $\bar{x} = 1.44$ ), eye row I width 1.8–2.1 ( $\bar{x} = 1.98$ ). *Legs*: Leg formula 4-1-3-2; patella-tibia III shorter than IV. Patella-tibia I length 2.3–3.2 ( $\bar{x} = 2.70$ ).

*Female*: ( $n = 5$ ). Total length 6.5–9.9 ( $\bar{x} = 7.90$ ), length of carapace 3.0–3.8 ( $\bar{x} = 3.38$ ), maximum carapace width 2.2–2.7 ( $\bar{x} = 2.44$ ), eye field length 1.3–1.7 ( $\bar{x} = 1.52$ ), eye row I width 2.0–2.3 ( $\bar{x} = 2.14$ ). *Legs*: Leg formula 4-3-1-2; patella-tibia III shorter than IV. Patella-tibia I length 2.0–2.6 ( $\bar{x} = 2.36$ ).

**Material examined.**—**MARSHALL ISLANDS**: *Majuro*, 1♂1♀1imm (JWB & JAB). **CAROLINE ISLANDS**: *Palau*, Angaur, 1♀ (JWB & ERB); *Helen Reef*, 1♂1♀1imm (JWB & ERB); *Koror*, 8♂10♀1imm (JWB, ERB & JAB). *Peleliu*, 1♀1imm (JWB & ERB); *Malakal*, 2♀ (JWB, ERB & JAB). *Yap*, 1♂3♀1imm (JWB, ERB & JAB). *Truk*, 1♀ (JWB & JAB). *Ponape*, 2♀1imm (JWB & JAB). **FIJI**: *Viti Levu*, 1♂2♀ (JWB, ERB & JAB). **AMERICAN SAMOA**: *Tutuila*, 1♂1♀ (JAB). **AUSTRALIA**: *Darwin*, 1♀ (JAB).

**Distribution.**—Mozambique, India, Sri Lanka, Singapore, Japan, China, New Guinea, Solomon Islands, Caroline Islands, Marshall Islands, Fiji, Samoa, Australia.





Figures 81–90.—The genus *Thorelliola*. 81–85, *Thorelliola ensifera* from the Marquesas Islands. 81, Left palp ventrally; 82, Palp laterally; 83, Epigynum; 84, Internal structure of epigynum—single spermatheca and ducts. 85, Abdominal pattern of female. 86–90, *Thorelliola dunicola* new species, from Ponape. 86, Left palp ventrally; 87, Palp laterally; 88, Epigynum; 89, Internal structure of epigynum—single spermatheca and ducts. 90, Abdominal pattern of female.

Genus *Thorelliola* Strand 1942

(*Thorellia* Keyserling 1882 preoccupied)

**Diagnosis.**—A fissidentate salticid with one 3–6 cusped retromarginal cheliceral tooth, two prolateral cheliceral teeth, one much smaller than the other. Metatarsi I with lateral spines, coxae one widely separated, anterior eye row strongly recurved.

*Thorelliola ensifera* (Thorell 1877)

Figs. 81–85

*Plexippus ensifer* Thorell 1877

*Thorellia ensifera* (Thorell): Keyserling 1882.

**Discussion.**—There is some evidence (Chelstowska pers. comm.) that the widespread Pacific salticid that has always gone by this name is not the same species as *Plexippus ensifer*, which was originally described from Celebes. We have taken it in a variety of habitats: in litter, on tree trunks, foliage and buildings, in forested and non-forested areas, and at elevations from 0–800 m.

**Measurements.**—*Male*: ( $n = 5$ ). Total length 4.4–4.8 ( $\bar{x} = 4.68$ ), length of carapace 2.1–2.3 ( $\bar{x} = 2.19$ ), maximum carapace width 1.6–1.8 ( $\bar{x} = 1.73$ ), eye field length 1.1–1.3

( $\bar{x} = 1.21$ ), eye row I width 1.5–1.7 ( $\bar{x} = 1.67$ ). *Legs*: Leg formula 1-4-2-3; patella-tibia III equal to IV. Patella-tibia I length 1.9–2.2 ( $\bar{x} = 2.02$ ).

*Female*: ( $n = 5$ ). Total length 3.7–4.3 ( $\bar{x} = 3.92$ ), length of carapace 1.7–1.8 ( $\bar{x} = 1.74$ ), maximum carapace width 1.3–1.9 ( $\bar{x} = 1.45$ ), eye field length 0.9–1.0 ( $\bar{x} = 0.97$ ), eye row I width 1.3–1.9 ( $\bar{x} = 1.44$ ). *Legs*: Leg formula 4-1-3-2; patella-tibia III equal to IV. Patella-tibia I length 1.1–1.3 ( $\bar{x} = 1.16$ ).

**Material examined.**—(all from our collection)

**MARIANA ISLANDS:** *Guam*, 6♂3♀, 7imm.

**CAROLINE ISLANDS:** *Palau*, 34♂31♀, 75imm;

*Yap*, 21♂39♀, 59imm; *Ulithi*, 2♂3♀, 1imm; Pon-

ape, 1♂4♀, 6imm. **MARSHALL ISLANDS:** *Eni-*

*wetok*, 16♂15♀, 31imm; *Kwajalein*, 15♂5♀,

12imm; *Majuro*, 6♂17♀, 28imm. **FIJI:** *Viti Levu*,

28♂27♀, 56imm. **AMERICAN SAMOA:** *Tutuila*,

6♂5♀, 17imm. **COOK ISLANDS:** *Aitutaki*,

5♂8♀, 13imm. *Rarotonga*, 38♂36♀, 97imm. **SO-**

**CIETY ISLANDS:** *Moorea*, 21♂15♀, 85imm.

**MARQUESAS ISLANDS:** *Fatu Hiva*, 8♂9♀,

19imm; *Hiva Oa*, 27♂38♀, 65imm; *Nuku Hiva*,

22♂17♀, 41imm.

**Distribution.**—Malaysia across the Pacific to the Marquesas Islands.

*Thorelliola dumicola* new species

Figs. 86–90

**Holotype.**—Male from Ponape (Caroline Islands), SW of Sekere Sch., shaken from bushes overhanging roadbank, 10 June 1973. Coll. J.A. Beatty & J.W. Berry.

**Etymology.**—The specific epithet, *dumicola*, means dwelling in thickets, because of the habitat in which the specimens were collected.

**Discussion.**—The placement of this species in the genus *Thorelliola* can be questioned because of its lack of the two strong recurved frontal spines characteristic of *T. ensifera*. However, the color pattern, while paler and less distinct in *dumicola*, is almost identical with that of light-colored and juvenile specimens of *T. ensifera*. Body shape and appendage proportions are similar in both species, and the genitalia are of the same form. The number and arrangement of spines on the appendages show only slight differences between the two species, and both have the unusual 3–6 cusped tooth on the cheliceral margin.

**Diagnosis.**—Differs from *T. ensifera* by its paler abdominal pattern, and in males by having only a single slender frontal bristle rather than two strong ones; recognizable by palp and epigynum (Figs. 86–89).

**Description.**—*Male*: ( $n = 1$ ). Total length 2.9, length of carapace 1.5, maximum carapace width 1.2, eye field length 0.8, eye row I width 1.2. Cephalothorax greyish-brown with somewhat lighter eye field and anterior, flat thorax; eye field rather bare, with small indistinct setae. Abdomen very different from the usual coloration of *T. ensifera*, resembling rather *Euophrys*, light whitish-yellow with indistinct pattern of yellowish-grey pigmented median and marginal spots, making indistinct chevrons in posterior half; dark bristles and setae more prominent. Frontal aspect: face brownish, eyes I surrounded with whitish setae, bristles on clypeus small and inconspicuous; chelicerae brownish; pedipalps whitish with yellow cymbium. *Legs*: Leg formula 4-3-1=2; patella-tibia III equal to IV. Patella-tibia I length 0.9. Legs I light yellow. *Palp*: Lacks the enlarged spines and somewhat angular cymbium in *T. ensifera*, but in form of palpal bulb and tibial apophysis the two are extremely similar (Figs. 86, 87).

*Female*: ( $n = 2$ ). Total length 3.1, 4.0;

length of carapace 1.5, 1.9; maximum carapace width 1.3, 2.0; eye field length 1.0, 1.1; eye row I width 1.3, 2.0. Cephalothorax yellow with brown shade, with a pair of brown spots on posterior slope of thorax. Small, colorless setae poorly visible on light background, however sparse, short dark bristles more distinct because of color contrast. Abdomen coloration like male (Fig. 90). Frontal aspect: face light yellow, eyes I surrounded with light yellow setae dorsally, ventrally whitish; chelicerae bulging basally, greyish-yellow, apically yellow. *Legs*: Relative leg length 4-3-1-2; patella-tibia III equal to IV. Patella-tibia I length 1.1, 1.4. Pedipalps and legs I yellowish-white with sparse dark setae. *Epigynum*: Of same form as that of *T. ensifera*, but with spermathecae smaller and ducts shorter (Figs. 83, 84; 88, 89).

**Material examined.**—CAROLINE ISLANDS: Ponape, SW of Sekere Sch., shaken from bushes along roadbank, 10 June 1973, 1♂ (the holotype) and 1♀imm (JAB & JWB) (BPBM). Mt. top, shaking, 6 June 1973, 1♀ (JAB & JWB).

**Distribution.**—Known only from Ponape in the Caroline Islands.

Genus *Trite* Simon 1885

**Discussion.**—Related species that have been redescribed by Žabka (1988) are *Trite auricoma* (Urquhart 1885), *T. pennata* Simon 1885, and *T. planiceps* Simon 1889. Seventeen species are currently placed in the genus (Prószyński 1990), all from Australia, New Zealand and south Pacific islands. Four of these, *T. rapaensis* Berland 1942 (Figs. 91–93), *T. ignipilosa* Berland 1924 (Figs. 94, 95), *T. lineata* Simon 1885 (Figs. 98–100), and *T. gracilipalpis* Berland 1929 (Figs. 101–104) are illustrated here for comparison with the new species and to make available more detailed illustrations than have been available before.

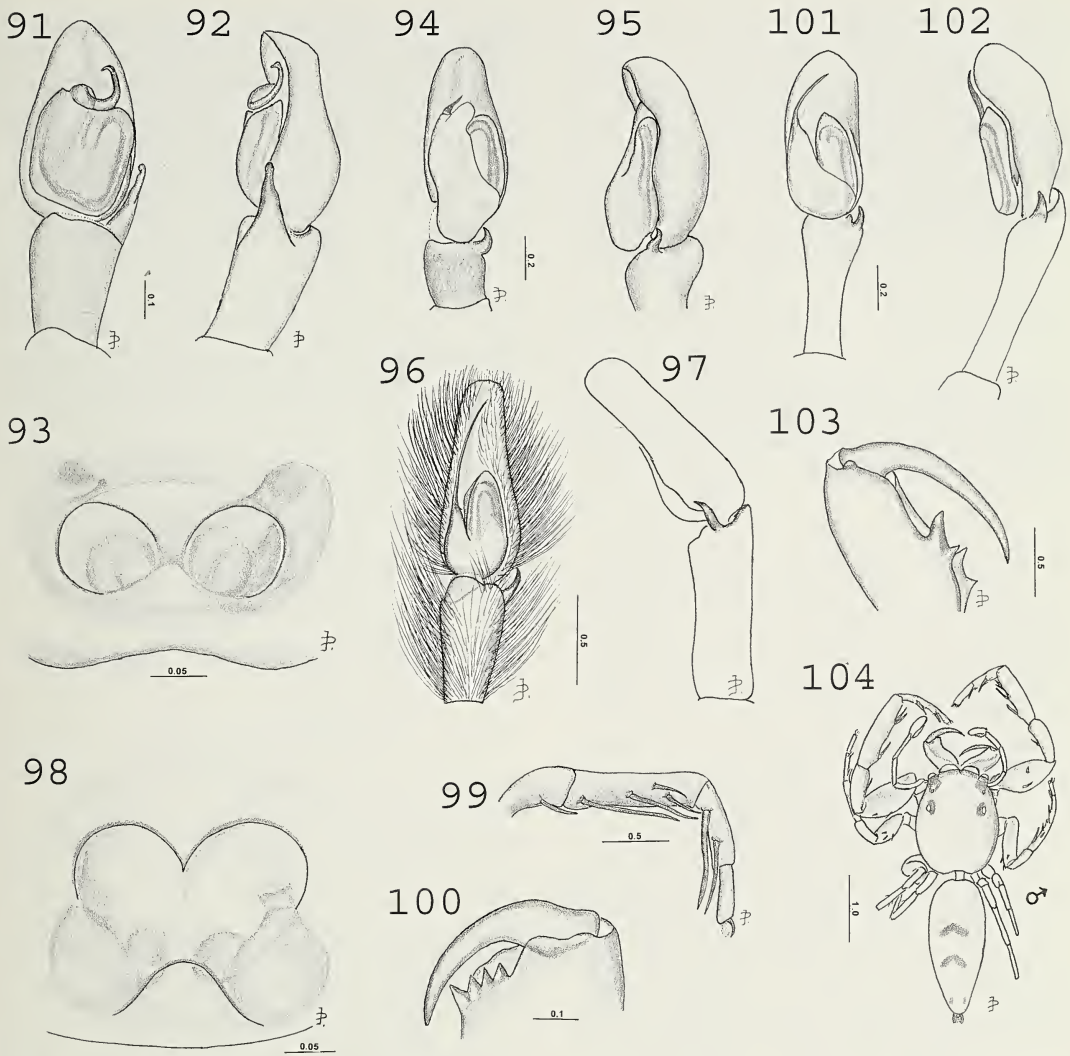
**Diagnosis.**—Medium-to-large fissident or plurident salticids with fourth leg longer than third, cephalic portion of the cephalothorax flat, second row of eyes closer to anterior than posterior row, anterior eyes nearly contiguous and ocular area wider behind than in front.

*Trite ponapensis* new species

Figs. 96, 97; Map 7

**Holotype.**—Male from Ponape, top of mountain, tree shaking, 6 June 1973 (J.W. Berry & J.A. Beatty) (BPBM).





Figures 91–104.—The genus *Trite*. 91–93, *Trite rapaensis*; 91, Left palp ventrally; 92, Palp laterally; 93, Epigynum. 94, 95, *Trite ignipilosa* from New Caledonia; 94, Left palp ventrally; 95, Palp laterally. 96, 97, *Trite ponapensis* new species from Ponape; 96, Left palp ventrally; 97, Palp laterally. 98–100, *Trite lineata* from Nouméa. 98, Epigynum; 99, Tibia I, female; 100, Ventral view of female chelicera; 101–104, *Trite gracilipalpis*. 101, Left palp ventrally; 102, Palp laterally; 103, Ventral view of chelicera; 104, Dorsal appearance of male (TYPE) from Loyalty Island.

**Etymology.**—The species is named for the island of Ponape in the Caroline Islands, the only known location.

**Discussion.**—This species is placed in *Trite* with considerable doubt. It is unidentate rather than fissidentate and the middle eye row is closer to the posterior than the anterior eyes. The general appearance is similar to *Bavia*, but both the cheliceral teeth and genitalia are quite different from that genus. In some respects it resembles *Thiania* C.L. Koch 1846

and the *Marpissa* C.L. Koch 1846 group of genera. With only a single specimen available we are unable to arrive at any firm conclusion.

**Diagnosis.**—Externally resembles *Bavia* Simon 1877 from which it differs by the structure of the palp, the straight dorsal edge of the palpal tibia and the cheliceral dentition. Distinguishable from other *Trite* by the long thin, nearly straight embolus which originates near the base of the bulb (Figs. 96, 97).

**Description.**—*Male*: ( $n = 1$ ). Total length



Map 7.—Distribution of five species of *Trite* in the Pacific. *Trite ponapensis* new species (□), *Trite gracilipalpis* (■), *Trite ignipilosa* (△), *Trite lineata* (▲), and *Trite rapaensis* (★).

9.5, length of carapace 4.1, maximum carapace width 3.0, eye field length 2.1, eye row I width 2.5. Cephalothorax broad but more elongate and less swollen than in *Bavia*; light brown, dorsum of thorax with broad lighter zone with minute whitish setae, fovea prominent. Eye field light greyish-brown, finely rough, slightly shiny, with a line of whitish setae along lateral eyes and above eyes I. Sides with sparse, inconspicuous brownish setae, longer and denser under lateral eyes along a crest reminiscent of *Ascylltus*. Abdomen long and thin, broadest anteriorly, gradually narrowing and pointed posteriorly, with long spinnerets. Median area of dorsum whitish, margins brown, sides with dense thin brown lines on white background; spinnerets light yellow. Frontal aspect—face light reddish-brown, rims of eyes I black surrounded with inconspicuous white-tipped setae. No contrasting spots. A line of long brown setae below AME overhanging cheliceral bases, chelicerae reddish-brown with papillate surface. ALE almost touching AME, diameter of AME = 2 diameters of ALE. One retrolateral cheliceral tooth, two prolateral cheliceral teeth. Ventral aspect: Endites elongate, rectangular, rounded apically, narrowing basally, without any depression or separate expansion along external edge. Chelicerae, endites, and labium fawn, anterior coxae light brown, coxae II-IV whitish-yellow; sternum yellow, darker marginally; abdomen ventrally greyish-white with light brown epigastric fold, light grey rectangular area along majority of length of abdomen, no dark ring around spinnerets. Pedi-

palps with dense brush of long grey setae along edges of patella, tibia and cymbium, no such characters in any *Bavia*. Pedipalps long and thin, yellowish-brown, extremities of segments slightly lighter, but no contrasting spots. Dorsal anterior edge of pedipalpal tibia triangular. *Legs*: Leg formula 1-4-2-3, patella-tibia III shorter than IV. Patella-tibia I length 4.2. Legs I light brown, in some areas yellowish; femur I with prolateral surfaces bald and shiny, brown, with a crest of blackish setae along dorsal edge. Inconspicuous spot of whitish setae prolaterally on patella. Tibia I has one additional lateral spine between first and second ventral spines, slightly more dorsally, with all ventral prolateral spines concentrated in the apical half of the segment. *Palp*: See diagnosis and Figs. 96, 97.

*Female*: Female is unknown.

**Material examined.**—Only the holotype.

**Distribution.**—Known only from Ponape in the Caroline Islands.

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## THERAPHOSIDAE OF THE MOJAVE DESERT WEST AND NORTH OF THE COLORADO RIVER (ARANEAE, MYGALOMORPHAE, THERAPHOSIDAE)

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**ABSTRACT.** Two new species of *Aphonopelma* from the Mojave Desert are described, *A. joshua* and *A. mojave*. Four nominal species, *Aphonopelma iodium* (*A. iodius*), *A. melanium* (*A. melanius*), *A. angusi*, *A. nevadanum*, described from the Mojave Desert and the Great Basin are treated as a single species; *Aphonopelma iodium* (Chamberlin 1939) is proposed as the species name since it is one of two possible senior synonyms (the other, *A. melanium* (*A. melanius*) in the same publication) and is the specific name of the first Theraphosidae to be described from the Mojave Desert; *A. iodium* is redescribed. Generic, subgeneric, and specific characters previously used to separate *Aphonopelma* are reviewed. *Aphonopelma* is redefined; *Clavopelma* is removed from the synonymy of *Aphonopelma*. The status of the following eight species described prior to 1939 with type localities either in the United States or in Baja, California is discussed: *Aphonopelma californica*, *A. leiogaster* (Doleschall), *A. steindachneri* (Ausserer), *A. rusticum*, *A. marxi*, *A. helluo* (Simon), *A. rileyi* (Marx), and *A. pseudoroeseum* (Strand). *Aphonopelma steindachneri*, *A. rusticum*, *A. marxi*, and *A. helluo* are considered as valid species; *A. californica*, *A. leiogaster*, *A. rileyi*, and *A. pseudoroeseum* are considered as *nomina dubia*.

The *Aphonopelma* of North American are poorly known. Although many species have been described few specimens can be properly identified either by using available keys or by wading through species descriptions. Most identifiable specimens belong to species found in Mexico or Central America that are easily recognized by unique color patterns, such as that of *A. seemanni*. Correct identification of specimens collected within the United States is often suspect since determinations must be based on the process of elimination using collection dates and locality data in combination with coloration, coxal setation, and metatarsal scopulation.

Chamberlin & Ivie (1939), Chamberlin (1940) and Smith (1994) described the majority of the currently recognized *Aphonopelma* species. Since many of their descriptions were based on one or two specimens variational limits were unknown to them with the consequential result of species determination by highly variable, artificial characters. It is my intention in this paper to describe the theraphosid species of the Mojave Desert using reliable taxonomic characters, established as such only after thorough analyses of variation within each putative species. Ecological, geo-

graphical, and behavior data are included and support morphologically-based species determinations.

The species redescribed here, *A. iodium*, belongs to a species group that are virtually impossible to differentiate by unaided visual examination: all are very similar in size, color, and extent of metatarsal scopulation and all share a common fall breeding season (breeding season determination was based on the time of year that both type males and males from type localities were collected). I will refer to the group collectively as 'eutylenum types' or as the 'eutylenum group' since *A. eutylenum*, as member of this assemblage, is referred to in the literature more than any of the other species and since preliminary data suggest that many of these species (other than those considered *A. iodium*) belong to a single widely distributed species, in which case *A. eutylenum* would be considered the senior subjective synonym based both on page priority and usage in the literature.

### METHODS

All specimens analyzed in this study were mature individuals. Males of the different species were collected while searching for fe-

males during their respective breeding seasons. Breeding season is defined as the period of time between which the first males of a given species abandon their burrows, becoming itinerants, and the vast majority have died from senescence or predation to the point that individuals are rarely found until the following year. The majority of males collected were taken between the years 1989–1993; and borrowed specimens other than types were collected as early as 1966. The system for collection was to drive slowly down least traveled backroads or powerline roads on a weekly basis (often 2–3 days a week) starting 1–2 weeks before the perceived beginning of a particular breeding season and ending when no males were found for two consecutive weeks.

The east and west Mojave Desert are defined as east and west, respectively, of a north-south line through Death Valley, Silurian Valley, Silver Dry Lake, Soda Dry Lake, the Bristol Mountains, Devil's Playground, Bristol Dry Lake, Cadiz Valley, and Danby Dry Lake. Joshua Tree National Park and Death Valley National Park are, respectively, referred to as Joshua Tree National Monument and Death Valley National Monument in this manuscript because they were so-named while this study was in progress.

Measurements were performed using an American Optical 570 stereomicroscope equipped with an eyepiece micrometer. Measurements are all in millimeters and are accurate to 0.05 mm except for tarsal measurements which are accurate to 0.1 mm. Leg and pedipalp measurements were taken from the left side unless some or all segments of a given leg were missing or it was apparent that an appendage was in the process of regeneration. All segment measurements were performed from the retrolateral aspect; this measurement equal to the distance from the proximal point of articulation to the distal most point of the segment (Coyle 1971, 1989). Carapace and sternum lengths were taken with anterior and posterior margins in the same horizontal plane; width measurements were performed in the same fashion. Measurements of femur width in males were taken from the dorsal aspect at the widest pro- to retrolateral point other than at the base; in femur I & IV that point is preapical of its articulation with the patella; in femur III that point is basad of the

preapical point for femur I in the distal half of the segment. Extent of metatarsal scopulation was determined by using maximum extent of complete metatarsus I scopula as the proximal point for measurement in metatarsi II–IV.

Because tarsal measurements were difficult to perform without removing much of the distal scopulae and claw tufts, measurements were performed by depressing the apical scopulae and claw tufts against the integument with a flattened forceps. Because of a greater possibility of error in measuring the tarsi, leg I–IV ratios were calculated by adding the lengths of the femur, patella, tibia, and metatarsus only to represent the length of each leg; palp length was calculated by adding the lengths of the femur, patella, and tibia only. Cheliceral length measurements also were difficult to perform because of relaxation and over-extension of chelicerae as a result of preservation. These measurements were omitted except in type specimens of *A. joshua* new species and *A. mojave* new species because accurate measurements generally required dissection of chelicerae and because in living conspecific specimens chelicerae can be relatively more distended in some individuals of a smaller size than in other individuals of a larger size. Abdominal measurements were also omitted, except in type specimens and in largest and smallest specimens, due to dependence of abdominal size on nutritional state of the specimen. Carapace length was found to be the most reliable indicator of overall size.

All ink drawings were done with the aid of a camera lucida fitted on a Wild Heerbrugg M5 stereomicroscope. Spermathecae were cleared in 20% NaOH prior to illustration. Scanning electron micrographs were taken with a JEOL JSM C35 scanning electron microscope.

Characters and quantitative character values in Tables 1 and 2 are an essential part of each species description. These tables should be referred to unless specific values are given in the text.

**Specimens examined.**—Specimens examined other than samples of the species described here, are as follows: types: *Clavopelma tamaulipeum*, *Chaunopelma radinum*, *Aphonopelma angusi*, *A. iodum* (*iodius*), *A. melanum* (*melaninus*), *A. nevadanum*, *A. eutylum*, *A. paloma*, *A. phanus*, *A. phasmus*, *A. reversum*, *A. simulatum*, *A. zionis*



(AMNH), *Eurypelma steindachneri* [syntype-BMNH and (2) presumed types-NHMH], *E. rusticum* [cotype #1585, 47(36)-USNM], non-types: *E. marxi* [45(30), 43(20)-USNM] and *E. helluo* [50(44)-USNM], and specimens from the type localities of the following species: *A. anax*, *A. apacheum*, *A. behlei*, *A. brunnium* (*brunnium*), *A. chalcodes*, *A. clarum*, *A. coloradanum* (*coloradana*) *A. cratium* (*cratius*), *A. cryptethum* (*cryptethus*), *A. echinum* (*echina*), *A. helluo*, *A. lithodonum*, and *A. seemanni*.

**Abbreviations used.**—*Spination abbreviations*: a = apical; b = basal; d = dorsal half; e = preapical; Fe = femur; L = left; m = medial; Me = metatarsus; p = prolateral direction; Pt = patella; r = retrolateral direction; R = right; Ti = tibia; v = ventral half; 0.25, 0.80, etc. = approximate location of a spine taken as a fraction of the segment length from the proximal end.

*Tabular character table abbreviations*: Atten = attenuate; bas swln = basally swollen; CxI = coxa I; E = east Mojave; LAI, LAII, LAIII, LAIV = lengths of legs I, II, III, IV, respectively; LC = carapace length; LFI, LFII, LFIII, LFIV, LFP = lengths of femora I, II, III, IV, palp, respectively; LMI, LMII = lengths of metatarsi I and II, respectively; LTI, LTII, and LTIV = lengths of tibiae I, II, and IV, respectively; par div = partially divided; retr bnd = retrolateral bend; S&Cx = sternal and coxal; ScMIV = scopula of metatarsus IV; ScTaIV = scopula of tarsus IV; sht = short; swln = swollen; undiv = undivided; unif = uniform; v = ventral; W = west Mojave; WC = carapace width; WCh = chelicerae width; WFI, WFII = widths of femora I and II, respectively; WS = sternal width.

*Museum abbreviations*: AMNH = American Museum of Natural History, New York; BMNH = The Natural History Museum, London; MNHN = Muséum National d'Histoire Naturelle, Paris; NHMW = Naturhistorisches Museum, Wien; USNM = National Museum of Natural History, Washington.

*Other abbreviations*: BDM = Beaver Dam Mountains, southwestern Utah; JTNM = Joshua Tree National Monument, California. Abbreviations for eyes are standard for Araneae.

## TAXONOMY

**Synonymy of *Rhecostica* = *Aphonopelma*.**—Raven (1985) placed the following genera

in the synonymy of *Rhecostica* Simon 1892, a senior subjective synonym of *Aphonopelma* Pocock 1901: *Aphonopelma*, *Dugesiiella* Pocock 1901, *Pterinopelma* Pocock 1901, *Delopelma* Petrunkevitch 1939, *Chaunopelma* Chamberlin & Ivie 1939, and *Clavopelma* Chamberlin 1940. He concluded that they shared the form of the double tibial spur and the thorn-like setae on the prolateral coxae and that there were no other characters known that merited their continued separation. Because of the extensive usage of *Aphonopelma* in the literature Levi & Kraus (1989) petitioned the ICZN to give *Aphonopelma* precedence over *Rhecostica*. By Opinion 1637 of the ICZN (June 1991) *Aphonopelma* was given precedence whenever the two were considered to be synonyms.

**Review of generic characters.**—Pocock (1901) erected six genera during his dismemberment of *Eurypelma*, two of which had members north of Mexico, *Aphonopelma* and *Dugesiiella*. These two genera were respectively distinguished by the absence and presence of a plumose scopula on the prolateral surface of femur I and the retrolateral surface of the palpal trochanter and by spiniform and thorn-like setae on prolateral coxa I. Petrunkevitch (1939) erected *Delopelma* which he differentiated from *Dugesiiella* by the complete absence of plumose hairs and from *Aphonopelma* by the presence of simple, recumbent hairs on coxae and trochanters. Chamberlin (1940) apparently recognized the presence of plumose setae in all genera and considered *Delopelma* (retaining only the type *D. marxi*) a subgenus of *Aphonopelma* based on the similar form of setae on prolateral coxa I. He, in turn, erected *Chaunopelma* which differed from both *Aphonopelma* and *Dugesiiella* by the presence of fine, soft prone hairs on the anterior coxa and trochanter of leg I and on the posterior palpal trochanter. Raven considered the differences in coxa I setation artificial.

Other than by the setation of prolateral coxa I and the form of the double tibial spur, Raven distinguished *Aphonopelma* (*Rhecostica*) by the following characters: scopula of tarsus IV integral (no setal division), an area of plumose or spatulate hairs on retrolateral maxillae or palpal trochanter, and males with a slender and tapering embolus. The type species of two of the genera in the synonymy of *Aphonopelma*

*ma*, *Clavopelma* and *Pterinopelma*, are endowed with setae on the retrolateral palpal trochanter that may be termed spatulate in form. In *Pterinopelma*, Pocock likened these setae to those found in *Euathlus* (*Brachypelma*) which are stout, finely plumose (often long plumed), and lanciform. Although less stout in *Clavopelma* these lanciform setae are distinctly different from the relatively slender, plumose, hair-like or spiniform setae (in some species finely plumose) of the remaining *Aphonopelma*.

Smith characterized *Aphonopelma* by the following: no organs of stridulation or plumose setae/hairs on trochanter or coxa of palp or leg I or on femur I, no plumose pad present on femur IV, a tapering embolus (more stout and shorter in material from Mexico and Central America) with a simple keel on dorsal surface or on apex (sometimes ribbed or toothed), spermathecae composed of separate seminal receptacles, integral tarsus IV scopula, scopula of metatarsus IV ranging from  $\frac{1}{5}$ – $\frac{2}{3}$ , and no swollen leg segments. One of the character distinctions that Smith used to separate *Euathlus* (*Brachypelma*) and *Aphonopelma* was the presence of plumose setae on the prolateral trochanter and basal femur of leg I in *Euathlus* and the presence of non-plumose setae in *Aphonopelma*. It is not clear whether Smith was referring to the absence of lanciform setae (believed to have a stridulatory function) in *Aphonopelma* or had not detected the plumose condition of the hair-like or spiniform setae in the genus. Smith removed *Aphonopelma paloma* from the genus as the type of his newly erected monotypic genus, *Apachepelma*, based on partial division by setae of the tarsus IV scopula in combination with small size. Of the known *Aphonopelma* species, only *A. joshua* shares this character combination with *Apachepelma paloma* although it is usually slightly larger (Table 1). However, both species are morphologically more similar to *A. mojave* (eastern race), a species in which the tarsus IV scopula is entire, than to each other. Males of an undescribed *Aphonopelma* species (females not known) from southeast Arizona appear to be, otherwise, very similar to *A. paloma* males except that in this species the tarsus IV scopula is entire. *Aphonopelma crinita* is a considerably larger species than *A. paloma* but also shows partial division of the tarsus IV scopula (Perez-Miles 1994). In size, prolateral coxal se-

tation, and palpal bulb morphology it is more similar to congeneric species with entire tarsus IV scopula than to the other species with partially divided scopulae. Because *Apachepelma* was erected on characters not recognized as generically significant and because the type species shares with *Aphonopelma* all characters diagnostic of the genus, *Apachepelma* is here considered a synonym of *Aphonopelma*. In addition to males of *A. paloma*, males of both *A. joshua* and eastern *A. mojave* have the third femur swollen to a degree that is easily recognized and that is non-overlapping with species in which the third femur is slightly swollen. The extent of the scopula of metatarsus IV within the genus was found to vary from a few scattered distal hairs (*A. paloma*) to over 80% scopulate distolaterally. Setation of the retrolateral femur IV in all *Aphonopelma* examined was found to be similar or identical to that of the prolateral femur I. Male emboli were found to have two marginal or lateral keels (usually indistinct in males with slender emboli) and one or two prominent medial keels.

Although Raven did not consider the form of setae on anterior coxa I to warrant generic division, it does appear to be of value in distinguishing species groups within those *Aphonopelma* in which males have a slender embolus. For instance, hair-like setae, as in *A. radinum*, are also characteristic of three similar small species, *A. paloma*, *A. joshua* (Fig. 7) and *A. mojave* (Fig. 8); basally swollen spiniform setae are characteristic of *A. iodinium* (Figs. 9, 10) and most other southwestern species; thorn-like, apically filiform setae, very distinct from the homologous setae of *A. iodinium*, are characteristic of most species east of Utah and Arizona. To my knowledge, specimens with thorn-like setae have not been collected in the United States west of Globe, Arizona.

**Critical review of subgeneric taxonomic characters.**—Chamberlin considered *Aphonopelma* to consist of three subgenera, *Delopelma*, *Gosipelma*, and *Aphonopelma*. *Delopelma* and *Gosipelma* were differentiated on the basis of the number of spines on the anterior face of the male palpal tibia (two and four, respectively). Several species within these subgenera were additionally distinguished by spination of the ventral palpal tibia and of the palpal patella. Smith (1994) also used spination characters in diagnoses of new



species. For example, he separated *A. chambersi* Smith from *A. cryptethum* Chamberlin by the presence of four and five prolateral spines, respectively, on the palpal tibia, differences in the shape of the posterior half of the basal segment of the palpal bulb, and differences in the shape of the cuspules on the labium. However, in *Aphonopelma paloma* the numbers of spines on the ventral and prolateral palpal tibia and on the palpal patella were shown to be variable and in all species described herein tibial and patellar spination varied more intraspecifically than between or among Chamberlin's *Delopelma* and *Gosipelma* species. For example, in *A. joshua* new species males (from one locality) the palpal tibiae were armed with 3–6 prolateral and 1–3 ventral spines and the palpal patellae with 0–2 spines; in *A. mojave* new species males tibiae were armed with 2–7 prolateral and 0–4 ventral spines and patellae with 0–2 spines; in *A. iodum* males (from BDM) tibiae were armed with 4–8 prolateral and 1–3 ventral spines and patellae with 0–3 spines. As a result of the high variability in spination, distinctions between species based on these characters are considered artificial differences.

Chamberlin separated *Aphonopelma* from *Delopelma* and *Gosipelma* by relative lengths of metatarsus and tibia I; "tibia I longer than metatarsus I" in *Delopelma* and *Gosipelma*; "tibia I not longer than metatarsus I, usually clearly shorter" in *Aphonopelma*. Males of both *A. joshua* new species and western *A. mojave* new species have been found in which the ratio is reversed from the usual condition; in both species tibia I can be longer than, equal to, or shorter than metatarsus I within a single population. These conditions invalidate the *Aphonopelma* subgeneric distinction. Although the length ratio of tibia I to metatarsus I has been discarded as a subgeneric character in this study it is taxonomically significant because it distinguishes the southern Utah population of *A. mojave* from other eastern populations, reveals generalities of reversal between *A. joshua* and western *A. mojave*, and is one of the quantitative characters that distinguishes *A. mojave* from *A. radinum* and *A. iodum* from similar types described prior to 1939.

**Critical review of specific taxonomic characters.**—All ocular characters used by Chamberlin to separate subgroups within the

subgenus *Aphonopelma* were found to be highly variable in this study and are considered to be artificial differences. For instance, *A. clarum* and *A. eutylum* were distinguished from the other *Aphonopelma* (subgenus) species in Chamberlin's key on the basis of "lateral eyes separated by the diameter of a posterior one or nearly so" versus separated "at most but little more than the radius of the posterior eye". Lateral eyes of the *A. eutylum* holotype are separated by approximately  $0.70 \times$  PLE length. This criterion would place two apparently conspecific Red Mountain, California males in separate species; distance between lateral eyes in one is  $0.44 \times$  PLE length and in the other is  $0.83 \times$  PLE length.

Specimen size and coarseness of setae on the anterior face of coxae were used by Chamberlin to separate *A. clarum* and *A. eutylum*. The ratio of carapace length of the former species to the latter is 0.73 which is less of a difference than the ratio of 0.66 for the smallest to largest *A. iodum* males from the BDM. Although size can be an important character in separating species, range values are needed before its discriminating value can be determined. The spiniform setae on prolateral coxa I in both *A. clarum* and *A. eutylum* are of the same form found in *A. iodum* (Figs. 9, 10). The coarseness of these setae was found to be relative to specimen size in *A. iodum* and their dispersion over the prolateral surface varied slightly within a given population.

Chamberlin used general color of legs and abdomen to separate *A. melanium* and *A. iodum*. The former holotype, collected in September toward the beginning of the breeding season, was described as "gunmetal brown or blackish", and the latter, collected in late November toward the end of the breeding season, was described as "lighter brown or yellowish". North American tarantulas are darker in color shortly after a molt than they are at any other time prior to a subsequent molt (pers. obs.). A reasonable assumption is that *A. melanium* was darker in color because it was collected closer to the time of its definitive molt than *A. iodum*, which had faded substantially by the time it was collected in late November. Although coloration can be a reliable character in separating some species, distinction between shades of a particular color can be highly subjective because of temporal changes in a specimen's color.

Table 1.—Males of *Aphonopelma*: Taxonomic characters and quantitative character values which separate the Mojave Desert *Aphonopelma* and distinguish them from the most similar species; °—species with hairlike setae on prolateral coxa I, distinguished by superscript only from *A. joshua*<sup>(1)</sup> and *A. mojave*<sup>(2)</sup>. \*—included in the synonymy of *A. idium*; <sup>1</sup>—no overlap with *A. joshua*; <sup>2</sup>—no overlap with *A. mojave*; <sup>3</sup>—no overlap with *A. idium*; [Type]—holotype; USNH—non-types, Marx collection. Mean and standard deviation shown in parentheses (8.33, 0.56). Abbreviations defined in Methods section of text. Carapace measurements are in millimeters.

	°joshua [n = 25]	°mojave [n = 42]	idium [n = 32]	°paloma [n = 9]	marxi [2-USNH]	simulatum (Type)	°radinum [Type]
LC	7.00–9.70 (8.33, 0.56)	6.70–9.60 (8.25, 0.72)	9.35–16.90 (13.0, 2.05)	<sup>21</sup> 4.10–6.20 (5.33, 0.51)	<sup>39</sup> 9.10 <sup>39</sup> 9.00	<sup>219</sup> 8.85	7.50
LTI/LMI	0.91–1.01 (0.97, 0.03)	0.92–1.07 (1.00, 0.04)	0.85–1.01 (0.92, 0.04)	<sup>1</sup> 1.04–1.11 (1.08, 0.02)	<sup>321</sup> 1.25 <sup>321</sup> 1.30	<sup>321</sup> 1.27	<sup>21</sup> 1.10
LTII/LMII	0.84–0.91 (0.87, 0.02)	0.86–0.96 (0.91, 0.02)	0.82–0.91 (0.87, 0.03)	0.88–0.94 (0.92, 0.02)	<sup>321</sup> 1.12 <sup>321</sup> 1.09	<sup>321</sup> 1.09	<sup>210</sup> 0.98
LFI/LTI	1.12–1.19 (1.15, 0.02)	1.18–1.28 (1.22, 0.02)	1.17–1.33 (1.24, 0.04)	<sup>1</sup> 1.22–1.31 (1.26, 0.03)	<sup>21</sup> 1.31 <sup>21</sup> 1.29	<sup>1</sup> 1.22	<sup>21</sup> 1.10
LFI/LTII	1.22–1.33 (1.25, 0.03)	1.30–1.41 (1.35, 0.02)	1.31–1.41 (1.36, 0.02)	<sup>1</sup> 1.41–1.53 (1.48, 0.04)	<sup>321</sup> 1.53 <sup>321</sup> 1.53	<sup>321</sup> 1.44	<sup>2</sup> 1.27
LFI/LMI	1.05–1.19 (1.12, 0.03)	1.15–1.29 (1.21, 0.04)	1.07–1.24 (1.15, 0.04)	<sup>1</sup> 1.28–1.40 (1.36, 0.04)	<sup>321</sup> 1.63 <sup>321</sup> 1.67	<sup>321</sup> 1.55	<sup>1</sup> 1.21
LFI/LMII	1.05–1.18 (1.10, 0.03)	1.16–1.31 (1.22, 0.04)	1.11–1.25 (1.18, 0.04)	<sup>1</sup> 1.28–1.42 (1.36, 0.04)	<sup>321</sup> 1.71 <sup>321</sup> 1.67	<sup>321</sup> 1.58	<sup>1</sup> 1.25
LAI/LC	3.06–3.58 (3.39, 0.11)	2.87–3.36 (3.07, 0.11)	2.95–3.46 (3.23, 0.11)	2.79–3.24 (3.09, 0.15)	<sup>321</sup> 2.82 <sup>312</sup> 2.87	<sup>321</sup> 2.81	3.19
LAI/LC	2.87–3.40 (3.25, 0.13)	2.70–3.18 (2.90, 0.10)	2.73–3.27 (3.05, 0.09)	2.58–2.98 (2.83, 0.13)	<sup>321</sup> 2.52 <sup>321</sup> 2.60	<sup>321</sup> 2.64	2.95
LAIV/LC	3.64–4.15 (3.89, 0.13)	3.11–3.71 (3.34, 0.12)	<sup>13</sup> 3.09–3.60 (3.42, 0.10)	<sup>13</sup> 3.06–3.55 (3.36, 0.16)	<sup>321</sup> 2.88 <sup>321</sup> 2.96	<sup>321</sup> 2.94	3.41
LAI/LAIV	<sup>20</sup> 0.81–0.89 (0.87, 0.02)	<sup>10</sup> 0.90–0.95 (0.92, 0.01)	<sup>10</sup> 0.92–0.96 (0.94, 0.01)	<sup>10</sup> 0.90–0.95 (0.92, 0.01)	<sup>3210</sup> 0.97 <sup>3210</sup> 0.97	<sup>210</sup> 0.96	<sup>10</sup> 0.93
LAI/LAIII	<sup>21</sup> 1.02–1.08 (1.04, 0.01)	<sup>11</sup> 0.99–1.14 (1.11, 0.01)	<sup>11</sup> 1.10–1.16 (1.13, 0.02)	<sup>21</sup> 1.15–1.19 (1.17, 0.01)	<sup>321</sup> 1.24 <sup>321</sup> 1.25	<sup>321</sup> 1.22	<sup>21</sup> 1.16
LAI/LP	<sup>22</sup> 2.28–2.42 (2.35, 0.04)	<sup>12</sup> 2.04–2.23 (2.12, 0.05)	<sup>12</sup> 2.05–2.21 (2.12, 0.04)	<sup>1</sup> 1.96–2.07 (2.02, 0.04)	<sup>321</sup> 1.87 <sup>321</sup> 1.90	<sup>321</sup> 1.85	<sup>12</sup> 2.21
WFIII/WFI							
swln ≥ 1.19 normal ≤ 1.15	swln	normal (W) swln (E)	<sup>1</sup> normal	swln	<sup>1</sup> normal	<sup>1</sup> normal	<sup>1</sup> normal
Scopula	<sup>3</sup> distal	distal	<sup>21</sup> distal	<sup>21</sup> distal	<sup>3</sup> distal	<sup>3</sup> distal	distal
MIV (%)	25–50	25–55	70–85	0–20	40, 45	35	45
Division	<sup>2</sup> par div	<sup>1</sup> undiv	<sup>1</sup> undiv	<sup>2</sup> par div	<sup>1</sup> undiv	<sup>1</sup> undiv	<sup>1</sup> undiv
Sc TaIV (%)	25–60			50–100			
S & Cx(v) setae	<sup>2</sup> sht, stout, conicform	<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten
Cx I setae prolateral	bas unif hairlike	bas unif hairlike	<sup>21</sup> bas swln spinifm	bas unif hairlike	<sup>21</sup> bas swln spinifm	<sup>21</sup> bas swln spinifm	bas unif hairlike
Palpal bulb	<sup>2</sup> retr bnd uniform	<sup>1</sup> retr bnd angular	<sup>2</sup> retr bnd uniform	<sup>2</sup> retr bnd uniform	<sup>2</sup> retr bnd uniform	<sup>2</sup> retr bnd uniform	<sup>1</sup> retr bnd angular
Carapace color	black	black	<sup>21</sup> paper-bag brown	black	chestnut	chestnut	chestnut and black

Smith (1994) described 25 new species of *Aphonopelma*, 14 of which were described from single specimens, eight from two specimens each, and only three from several specimens each. Most of these descriptions were based on taxonomic characters that either were determined to be highly variable intra-specifically and widely overlapping interspecifically or are subjective in nature. Characters most consistently used in his diagnoses were



Table 1.—Extended.

<i>phasmus</i> [Type]	<i>zionis</i> [Type]	<i>*melanium</i> [Type]	<i>iodium</i> [Type]	<i>*angusi</i> [Type]	<i>*nevadanum</i> [Type]	<i>helluo</i> [USNH]	<i>rusticum</i> [cotype]
<sup>3</sup> 8.20	<sup>2</sup> 9.70	<sup>21</sup> 13.50	<sup>21</sup> 14.30	<sup>21</sup> 10.70	<sup>21</sup> 15.90	<sup>321</sup> 17.30	<sup>21</sup> 14.10
<sup>31</sup> 1.04	1.01	0.94	0.94	0.97	<sup>21</sup> 0.87	<sup>31</sup> 1.03	—
<sup>31</sup> 0.93	0.91	0.86	0.89	0.91	<sup>2</sup> 0.85	<sup>31</sup> 0.94	0.89
<sup>21</sup> 1.17	<sup>321</sup> 1.15	<sup>1</sup> 1.25	<sup>1</sup> 1.22	<sup>1</sup> 1.23	<sup>1</sup> 1.27	<sup>321</sup> 1.35	—
1.33	1.31	1.36	1.33	<sup>1</sup> 1.38	1.32	<sup>321</sup> 1.46	<sup>1</sup> 1.41
<sup>1</sup> 1.22	1.15	1.17	1.15	<sup>1</sup> 1.20	1.10	<sup>321</sup> 1.38	—
<sup>1</sup> 1.24	<sup>1</sup> 1.19	1.16	1.18	<sup>1</sup> 1.25	<sup>21</sup> 1.13	<sup>321</sup> 1.36	<sup>1</sup> 1.25
3.25	3.30	3.21	<sup>2</sup> 3.39	3.29	3.24	<sup>321</sup> 2.80	—
3.02	3.05	3.06	3.20	3.07	3.12	<sup>321</sup> 2.67	<sup>321</sup> 2.57
3.55	<sup>1</sup> 3.56	<sup>1</sup> 3.40	<sup>1</sup> 3.55	<sup>1</sup> 3.45	<sup>1</sup> 3.42	<sup>321</sup> 3.02	<sup>321</sup> 2.96
<sup>31</sup> 0.91	<sup>1</sup> 0.93	<sup>1</sup> 0.94	<sup>21</sup> 0.96	<sup>1</sup> 0.95	<sup>1</sup> 0.95	<sup>1</sup> 0.93	—
<sup>21</sup> 1.15	<sup>21</sup> 1.16	<sup>1</sup> 1.13	<sup>1</sup> 1.14	<sup>21</sup> 1.16	<sup>1</sup> 1.11	<sup>1</sup> 1.13	—
<sup>1</sup> 2.09	<sup>1</sup> 2.15	<sup>1</sup> 2.11	<sup>1</sup> 2.18	<sup>1</sup> 2.08	<sup>1</sup> 2.17	<sup>321</sup> 1.95	—
<sup>1</sup> normal	<sup>1</sup> normal	<sup>1</sup> normal	<sup>1</sup> normal	<sup>1</sup> normal	<sup>1</sup> normal	<sup>1</sup> normal	<sup>1</sup> normal
<sup>321</sup> distal 60	<sup>321</sup> distal 65	<sup>21</sup> distal 72	<sup>21</sup> distal 79	<sup>21</sup> distal 70	<sup>21</sup> distal 71	<sup>321</sup> distal 60	<sup>21</sup> distal 0.75
<sup>1</sup> undiv	<sup>1</sup> undiv	<sup>1</sup> undiv	<sup>1</sup> undiv	<sup>1</sup> undiv	<sup>1</sup> undiv	<sup>1</sup> undiv	<sup>1</sup> undiv
<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten	<sup>1</sup> long, atten
<sup>21</sup> bas swln spinifm	<sup>21</sup> bas swln spinifm	<sup>21</sup> bas swln spinifm	<sup>21</sup> bas swln spinifm	<sup>21</sup> bas swln spinifm	<sup>21</sup> bas swln spinifm	<sup>21</sup> bas swln spinifm	<sup>21</sup> bas swln spinifm
<sup>2</sup> retr bnd angular	<sup>2</sup> retr bnd uniform	<sup>2</sup> retr bnd uniform	<sup>2</sup> retr bnd uniform	<sup>2</sup> retr bnd uniform	<sup>2</sup> retr bnd uniform	<sup>2</sup> retr bnd uniform	<sup>2</sup> retr bnd uniform
<sup>21</sup> light brown	<sup>21</sup> light brown	<sup>21</sup> yellow gray	<sup>21</sup> pale buff	<sup>21</sup> yellow gray	<sup>21</sup> golden yellow	—	—

shape of the basal division of the palpal bulb,  
extent of metatarsus IV scopula, number and/  
or position of megaspines of the lower process  
of the tibial spur, and prolateral spination of  
the palpal tibia. Of these characters the shape

of the basal division of the palpal bulb was  
weighted most heavily in separating males of  
new species. In examining the *Aphonopelma*,  
including type and non-type males and males  
collected from the type localities of 12 nom-

inal species, I found relatively minor variation in the general shape (form) of the basal division. Intraspecific variation (also see Perez-Miles 1989) was found to be as great as interspecific variation in all species described herein and in the following species: *A. paloma*, *A. reversum*, *A. chalcodes*, and *A. coloradanum* (Canon City, Colorado). Conversely, males of three very dissimilar species (*A. iodium*, *A. reversum*, and *A. coloradanum*) were found in which corresponding divisions of the bulb were nearly identical. Major differences, such as in several illustrations by Smith, may have been the result of molting difficulties, damage to the bulb (through the effects of preservation or during the immediate post-molt sclerotization process), or genetic mutation but are only doubtfully indicative of species distinctions, especially in light of locality data.

A second primary character that Smith used to diagnose males was the number and/or position of stout apical or subapical megaspines on the lower process of the male tibial spur. In *A. mojave* the inner megaspine (preapical spine on the inner or concave surface of process) was always present while the outer megaspine (spine on the outer or convex surface of process) was frequently absent; both spines varied considerably in size, shape, and their position on the process, their articulation varying from almost apical to decidedly preapical. One or more less stout apical spines were occasionally present between the larger megaspines. On the upper process the armature was also found to be variable; the inner surface of the process was always equipped with one megaspine but occasionally with two subequal megaspines and/or one to several additional lesser spines. A similar degree of variation was also found in both *A. joshua* new species and *A. iodium*.

The extent of the scopula of metatarsus IV (weighted heavily by Smith) proved to be a reliable character in this study after range values were established, especially in combination with size and color characters and locality data. Length values from museum specimens were often difficult to determine because much of the metatarsal pubescence and scopulae had been worn away through repetitive examination. However, under high magnification scopular extent could usually be determined by cuticular examination. In species

such as *A. iodium* the lateral extent of the scopula was found to be greater than the medial extent but this condition appeared to have been overlooked by Smith in his measurements of various type specimens. For the Chamberlin holotypes, *A. angusi*, *A. iodium*, *A. melanium*, and *A. nevadanum*, Smith illustrated the approximate extent of metatarsus IV scopula as, the distal 35, 40, 60, and 60% of the segment, respectively. According to Smith's criteria, this placed the former two species in a different species group than the latter two species. My own measurements of metatarsus IV scopula of the same holotype specimens are as follows (in approximate percentage): *A. angusi*, 40 medial, 70 retrolateral; *A. iodium*, 50 medial, 80 retrolateral; *A. melanium*, 50 medial, 70 retrolateral; *A. nevadanum*, 60 medial, 70 retrolateral. For the species *A. iodium* (not including above types) scopula extent ranged from 40–60% medially and from 70–85% retrolaterally (maximum extent). Medial extent was usually greatest in *A. joshua* and *A. mojave* and in both ranged from 25–50%.

Other male characters that Smith considered of lesser weight included number of megaspines of the upper process of the tibial spur, prolateral spination of tibia I, shape of the labial and maxillary (used less often) cuspules, condition of distal embolus (keeled or not), shape of the embolus tip, and shape of the posterior half of the palpal bulb (basal portion of the middle division). The number of labial cuspules in *A. joshua* varied from 33–78, in *A. mojave* from 26–90, and in *A. iodium* from 70–140 (in specimens collected from one locality). Distribution of the cuspules, hence, shape of the distribution varied considerably within all three species with substantial interspecific overlap. Differences in this character are considered to be artificial due to high variability in number and distribution and to the subjective nature in the interpretation of such highly irregular shapes.

The shape, orientation, and keeled condition of the embolus have been found to be relatively constant in males with slender emboli; shape and orientation are essentially as in the palpal bulbs in Figs. 14–21, 29–44 and as described below under the additional diagnostic characters for *Aphonopelma*. Even in such diverse species as *A. reversum*, *A. behlei*, and *A. coloradanum* the apical emboli were



often indistinguishable and the accentuation of the median keel no more variable interspecifically than intraspecifically. No males examined in this study were found with significant variation in embolic characters. Rather than attributing the major differences described and illustrated by Smith as characteristic of new species, I would suggest that such conditions were anomalies resulting from genetic abnormalities, molting problems, or damage to bulbs. If they were representative shapes then such species are indeed rare and distinguished only by the condition of the embolus.

The basal portion of the middle division of the palpal bulb was found to be variable within all species described here, primarily in the region of the basal cuticular protrusion (proximal prolateral protuberance) of the prolaterodorsal surface. Interspecific variation in this character was found to be greater between some species than intraspecific variation within the compared species (Figs. 14–21, odd numbered figures) although was negligible between ‘*eutylum* types’ (Figs. 29–44, even figures) and between several other species such as *A. coloradanum* and *A. reversum*.

In diagnosing females Smith primarily used two characters, shape of the spermathecae and scopulation of metatarsus IV; other characters used were setation of prolateral coxa I and spination of the palpal tibia. Spermathecae of six *A. iodum* females (two from one locality and two from a second locality) in Figs. 45–50 illustrate conspecific variation. Spermathecae of two other species, *A. joshua* and *A. mojave*, are illustrated in Figs. 22–28 to show interspecific similarity as well as intraspecific variation. Clearly, shape of the spermathecae can vary considerably within a species but, conversely, can be very similar among females of different species. Consequently, this character is not considered to have specific discriminating value.

**Primary taxonomic characters.**—In this study the taxonomic characters with the highest discriminating value were present in both genders; they are: (1) form of setae on the prolateral face of coxa I, (2) extent of metatarsal scopulation (primarily, metatarsus IV), (3) condition of tarsal scopula (entire or divided), (4) lengths of both legs III and IV relative to length of leg I, (5) lengths of both leg III and IV relative to carapace length, and (6) color of the carapace (in living specimens).

Additional characters that were weighted heavily separated males only; they are: (1) lengths of tibia I and metatarsus I relative to each other, (2) lengths of tibia II and metatarsus II relative to each other, (3) lengths of both tibiae I and II relative to femur I, (4) lengths of both metatarsi I and II relative to femur I, and (5) condition of femur III (swollen or normal).

**Status of some old ‘*Eurypelma*’ species.**—I have included eight *Aphonopelma* species in this study (seven with type localities in the U.S. and one from Baja California) that were described prior to 1939 (described as *Theraphosa* or *Eurypelma*) because of the possibility of synonymy in name with *A. iodum* and/or *A. mojave* which would preclude the use of one or both as species names for the Mojave Desert tarantulas; they are as follows: *Theraphosa californica*, *T. leiogaster* Doleschall 1852 (*Eurypelma*, in Ausserer 1871), *E. steindachneri* Ausserer 1875, *E. rileyi* Marx 1888, *E. rusticum*, *E. marxi*, *E. helluo* Simon 1891, and *E. pseudoroseum* Strand 1907. Although all of these species are now considered *Aphonopelma* (consult Raven 1985), I will refer to them in this section as *Eurypelma*.

*Eurypelma rileyi* was described on the basis a single female, type locality, Santa Barbara, California. The type is believed to no longer exist (N.I. Platnick, pers. comm. 1995) although Smith (1994) redescribed the species from a specimen in the USNM, maintaining that it was the female holotype. In my examination of the specimen, I found the spination armature (of all legs) to be grossly incongruent with that described by Marx, leg IV slightly greater than, rather than slightly shorter than, the carapace length (if Marx included coxa IV in his measurement), and no indication on the labeling that the specimen was part of the Marx collection (no data other than that on the label exists). Given these conditions, the likelihood that this specimen is the type of *E. rileyi* is controvertible. In addition, the epigastric region is missing rendering the gender of the fragmented alcohol specimen indeterminate (the specimen was formerly pinned and dried and the abdomen stuffed with cotton wool).

The carapace color of *E. pseudoroseum* was described as reddish-yellow or pinkish (translation), an obvious condition in living specimens but one almost impossible to determine

in specimens preserved for any length of time. Unfortunately, types of *E. pseudoroseum* (two females) do not exist and except for carapace color the species description could be equally applicable to a number of species.

A male (#1589-BMNH) from the Koch collection, type locality Pecos River, Texas, was considered by D.J. Clark (1961) to be the specimen figured by Ausserer in his original description of *E. steindachneri* (the specimen is fragmented and is missing leg III and IV except for the right trochanter and femur of leg IV; leg II (R) and tibia and metatarsus IV (R) from a larger specimen(s) are mixed in with the type). Smith (1994) also considered this male to be the holotype, assuming that Ausserer described a male from Pecos River, Texas rather than from San Diego, California. In a personal communiqué that I received from Dr. Jurgen Gruber (NHMW) concerning two male and one female specimens labeled *Eurypelma californicum* the following information was conveyed: (1) the original labeling of the three Austrian specimens is feared to have been discarded but museum acquisition records state that two specimens are types of *E. steindachneri* (California: San Diego) although the presumed type series was mixed up with later material and (2) since Ausserer described both genders, the non-type specimen is suggested to be a male collected in California (circa 1892) which apparently was lumped together with the types. Upon examination of these specimens I discovered that one of the males and the female were, decidedly, the specimens on which Ausserer based his description of *Eurypelma steindachneri*. Carapace and leg measurements that I performed on both genders were in agreement with those of Ausserer's, the ocular deformity described of the type female was present in the NHMW female, and the dorsal coverage of the urticating patch and the relatively straight cut and armature of the apical superior tibial spur described of the type male were in congruence with the respective characters of the NHMW male. Contrarily, measurements that I performed on the BMNH specimen were not in agreement with those in Ausserer's original description. The coloration of the types, as described by Ausserer, is typical of males and faded females, respectively, of specimens I have collected near the Mexican border, just southeast of San Ysidro, Califor-

nia. The limited extent of the scopulae of metatarsi III and IV in these San Ysidro specimens is very diagnostic of this species (approx.-distal  $\frac{1}{2}$ - $\frac{2}{3}$  and  $\frac{1}{3}$  or less, respectively) and agrees both in character with the NHMW specimens (Ausserer did not include data on the extent of scopulae) and in the general locality data of specimens collected near the Mexican border and provided to Ausserer by Dr. Steindachner. The non-type male is of the same species as the types.

Additional information conveyed to me by Dr. Gruber is as follows: (1) of the original specimens of Doleschall, according to Doleschall, the type of *Theraphosa (Eurypelma) californica* (female) was a dry specimen and according to Ausserer that of *T. (Eurypelma) leiogaster* (male) was also a dry specimen and (2) types of these species no longer exist (also verified by Gertsch (1978) in a personal communication to W. Icenogle).

In the original description of *E. rusticum*, Simon noted type localities as both Ft. Yuma and Williams, Arizona. It is not entirely clear from which of these localities the described specimen was collected. The holotype and other material from Ft. Yuma are believed to have been lost or destroyed. However, a male in USNM (#1585, cotype, *E. rusticum*, Collection: Marx, type locality Williams, Arizona) may be one of the original specimens in Simon's series (there are also leg segments of a smaller specimen mixed in with the fragmented type; the male is missing the patella, tibia, metatarsus, and tarsus of leg I). Smith (1994), apparently unaware of the existence of the cotype, redescribed *Aphonopelma rusticum* based on "Simon designated paratype material from northern Mexico". Although Simon clearly stated in his description that the species also occurred in northern Mexico, Smith selected, as the lectotype, a specimen (#5873, male, MNHP-Paris) from Mazatlan, Mexico, a locality distinctly not in northern Mexico. Since this male is not believed to be of the same species as the cotype male (#1585), the precise identity of *E. rusticum* = *A. rusticum* is uncertain. Reexamination of all type material will be necessary before a lectotype can be objectively designated. The *A. rusticum* of Chamberlin (type locality, Apache Trail, Arizona) is clearly not the *E. rusticum* of Simon; Smith redescribed this species as *A. rothi*.



In his 1940 work, Chamberlin indicated that the name '*marxi*' had previously been used to cover several different species including *A. simulatum* (Chamberlin & Ivie 1939) and that the precise identity of the species would remain in question until either the types were critically restudied or ample material from the San Bernardino Mountains (California) was examined. The labeling of the Marx specimens, from which Simon described *E. marxi*, apparently indicated type localities of California: San Bernardino Mountains and New Mexico: Punta-del-Aqua (Marx' labeling was often suspect (Gertsch 1961)); Chamberlin discounted New Mexico as a type locality of *E. marxi* but, interestingly, considered June Springs, New Mexico a second locality for *A. simulatum* (male and female). Although no labeled *E. marxi* types are known to exist, two *E. marxi* non-type males in USNM (localities: 1-#43(20), California, 1-#45(30), New Mexico) from the Marx collection match, closely enough, Simon's original description of the species; the *A. simulatum* holotype is indistinguishable from these specimens in all characters examined (Table 1). Furthermore, I have spent a considerable amount of time collecting in and around the San Bernardino Mountains and have found no specimens exhibiting the combination of characters present in the non-type *A. marxi* and in the *A. simulatum* holotype. In light of the above, I suggest that Marx mislabeled one of two New Mexico specimens and conclude here that *Eurypelma marxi* = *Delopelma marxi* = *Aphonopelma marxi* is a valid species name, that the New Mexico male be considered the neotype, and that *A. simulatum* be considered a junior synonym of *A. marxi* (NEW SYNONYMY).

*E. helluo* = *Delopelma helluo* = *A. helluo* (Table 1) is also considered here as a valid species name represented by the holotype (#17707, MNHN, type locality, Cape Lucas, Baja California); only one other *A. helluo* specimen (examined) from the Marx collection (non-type male, USNM, #50(44), locality, Cape Lucas) is known to exist.

**Nomina dubia.**—Because of the inadequacy of the original *Eurypelma* descriptions which could be equally applicable to a number of species combined with the loss of type specimens and/or appropriately labeled non-type specimens from collections from which

types were described, *Theraphosa californica* = *E. californica* = *Dugesiella californica* = *Aphonopelma californica*, *E. rileyi* = *A. rileyi*, *T. leiogaster* = *E. leiogaster* = *A. leiogaster*, and *E. pseudoroseum* = *Delopelma pseudoroseum* = *A. pseudoroseum* should be considered as nomina dubia, "in the interest of promoting" nomenclatural stability.

#### Genus *Aphonopelma* Pocock

*Rhecostica* Simon 1892: 162 (type species by original designation *Homoeomma texense* Simon 1891). Suppressed as a senior synonym of *Aphonopelma* by ICZN Opinion 1637.

*Aphonopelma* Pocock 1901: 553 (type species by original designation *Eurypelma seemanni* F.O. Pickard-Cambridge 1897). First synonymized with *Rhecostica* by Raven 1985: 149.

*Dugesiella* Pocock 1901: 551 (type species by original designation *D. crinita* Pocock 1901). First synonymized with *Rhecostica* by Raven 1985: 152.

*Delopelma* Petrunkevitch 1939: 567 (type species by original designation *Eurypelma marxi* Simon 1891). First synonymized with *Rhecostica* by Raven 1985: 151.

*Gosipelma* Chamberlin 1940: 4 (type species by original designation *G. angusi* Chamberlin 1940). Originally described as a subgenus of *Aphonopelma*; never elevated to full genus status. First synonymized with *Rhecostica* by Raven 1985: 153.

*Chaunopelma* Chamberlin 1940: 30 (type species by original designation *Delopelma radium* Chamberlin & Ivie 1939). First synonymized with *Rhecostica* by Raven 1985: 151.

*Apachepelma* Smith 1994: 45 (type species by original designation *Aphonopelma paloma* Prentice 1992). NEW SYNONYMY.

**Diagnosis.**—The genus *Aphonopelma* is distinguished from all other genera by the following combination of characters: (1) no known external organs of stridulation (males do stridulate, however); (2) normal, relatively slender (hair-like or spiniform) plumose setae on pro-lateral trochanter and femur of leg I and on the retrolateral coxa and trochanter of palp (in some species these setae are finely plumose); no 'large' plumose (lanciform or spatulate) setae such as those on the prolaterobasal femur of leg I in *Euathlus* or those on the prolateral coxa of leg I in *Grammostola*; (3) type I urticating hair only; (4) corresponding segments of all legs approximately the same width in females; femur III in males of some species laterally swollen; (5) scopula of tarsus IV usually

entire, if divided then only partially and narrowly by line of setae; (6) setae of prolateral coxa I hairlike and not basally swollen (known only in small species), spiniform and basally swollen, or distinctly thornlike (apically filiform), with all forms at least distally plumose; (7) metatarsus I flexing against lower process of tibial spur, with either apex of spur contacting ventral surface of metatarsus or outer edge of spur in the apical half contacting the prolateral metatarsus; (8) lower (outer) process of tibial spur curving prolaterodistally and widening apically, usually equipped with at least one apical or preapical megaspine, and upper (inner) shorter process less stout basally, relatively uniform in diameter throughout its length, and equipped on its inner surface with at least one (several not uncommon) stout, basally articulated megaspine.

**Additional diagnostic characters.**—Based on preliminary data, (1) ventral retro-marginal setae of maxillae and ventral marginal setae of coxae (other than distal margins) similar in form (and usually size) to prolateral setae of coxa I, or, similar to other ventral setae of coxae (more common); (2) extent of metatarsus IV scopula usually from distal 20–85%, rarely less than 20% or with scattered scopula hairs (*A. paloma* and undescribed species from southeast Arizona); (3) anterior sternal margin smoothly procurved or rarely with a broad but slight medial projection; (4) labiosternal suture recessed; labium rising steeply from suture; (5) male embolus tapering with inward and ventral curve, with strong ventrally directed bend near apex (in all species with slender emboli), embolus either very slender with three apical keels (medial keel most prominent), or, relatively wide with four prominent keels of which the distomedial and proximomedial keels are either convergent or closely parallel just basad of apex, with proximomedial or convergent keel serrate

and/or extending the full or nearly full length of embolus in some species; (6) transition of valley between processes of tibial spur considerably offset (protruding) from longitudinal plane of tibia; (7) tibiae I and II of females with at least one ventral spine (other than apical), rarely none and then only in species where male embolus is relatively broad apically; usually also with at least one prolateral spine, rarely absent on tibia II; (8) paired spermathecae separated and with capitate bulbs, variable in shape.

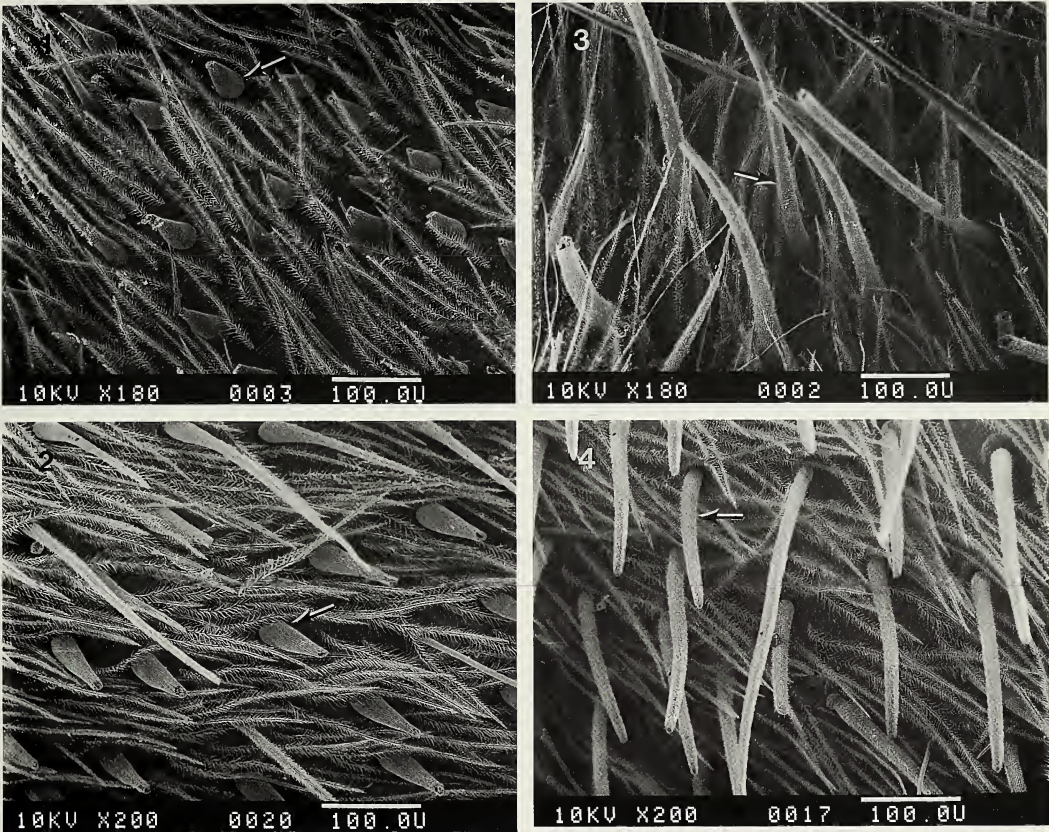
**Genera removed from synonymy.**—Two genera placed in the synonymy of *Aphonopelma*, *Clavopelma* and *Pterinopelma*, differ from the remaining *Aphonopelma* in characters here considered generic in value (above). *Clavopelma* Chamberlin (monotypic genus) is here removed from the synonymy of *Aphonopelma* because of the following differences: both types I and III urticating hairs, lanciform setae (similar to those in *Euathlus* (*Brachypelma*) but relatively smaller) on the prolateral trochanter and femur of leg I and on retrolateral trochanter of the palp, and a relatively straight (slender) embolus without a sharp ventrally directed bend near apex. *Pterinopelma* Pocock, as defined, is similar to *Euathlus* in the form of scopular setae on the posterior face of the palpal trochanter and the anterior face of the trochanter of leg I but dissimilar to both *Euathlus* and *Aphonopelma* in lacking a similar scopula of hairs on the anterior face of femur I. The presence of both types I and III urticating hairs, characteristic of *Euathlus*, is also characteristic of *Pterinopelma*. The anterior lateral eyes of *Pterinopelma* are proportionately larger relative to AME than in other genera in the synonymy of *Aphonopelma*. *Pterinopelma* is here not considered a synonym of *Aphonopelma* but its final disposition is reserved until all *Pterinopelma* species have been examined.

#### PARTIAL KEY TO MALES OF *APHONOPELMA*

Phylogenetic relationships are not implied by the couplets. Also, the asterisk (\*) indicates that key is for types only, and does not account for variation.

1. Setae on prolaeral coxa I hairlike, not basally swollen (Figs. 7, 8); small species . . . . . 2
- Setae on prolateral coxa spiniform, basally swollen (Figs. 9, 10) . . . . . 5





Figures 1–4.—Sternal and coxal setae, males (arrows indicate setae). 1, 2, *Aphonopelma joshua* new species; 1, Sternum, medial; 2, Coxa I, ventral, proximo-medial; 3, 4, *Aphonopelma mojave* new species; 3, Sternum, medial; 4, Coxa I, ventral, proximo-medial.

2(1).	Tarsus IV scopula as least partially divided by setae (Fig. 5).....	3
	Tarsus IV scopula complete, not divided by setae (Fig. 6).....	4
3(2).	Medial sternal setae hairlike or attenuate (refer to Fig. 3); Arizona .....	<i>paloma</i>
	Medial sternal setae short, stout, basally thickened, and coniciform (Fig. 1) .....	<i>joshua</i> new species
4(2).	Length ratios tibia I/metatarsus I, 0.92–1.07, femur I/tibia I, 1.18–1.28 (Table 1) .....	<i>mojave</i> new species
	Both ratios = 1.10 (Table 1); California, Manhattan Beach (type locality doubtful) ...	<i>*radinum</i>
5(1).	Extent of metatarsus IV scopula less than distal 40% .....	6
	Metatarsus IV scopula at least distal 55% .....	7
6(5).	Carapace length >13 mm; California, Baja; in life carapace and legs medium brown to black .....	<i>*steindachneri</i>
	Carapace length <10 mm; Utah, New Mexico .....	( <i>stimulatum</i> ) = <i>*marxi</i>
7(5).	Scopula metatarsus IV, distal 55–65% .....	8
	Scopula metatarsus IV ≥ distal 70% .....	10
8(7).	Palpal bulb retrolateral bend uniform (as in Figs. 14, 29) .....	9
	Bulb with retrolateral bend angular (as in Fig. 18); Grand Canyon, Phantom Ranch ..	<i>*phasmus</i>
9(8).	Length carapace <10 mm; length ratio leg IV/carapace approximately 3.6; Arizona ....	<i>*zionis</i>
	Length carapace >15 mm; length leg IV/carapace approximately 3.0; Baja .....	<i>*helluo</i>
10(7).	Length ratio leg IV/carapace = 3.09–3.60; California .....	<i>iodium</i>
	Ratio leg IV/carapace <3.0; Arixon, Mexico .....	<i>*rusticum</i>



PARTIAL KEY TO FEMALES OF *APHONOPELMA*

Phylogenetic relationships are not implied by the couplets. Also, the asterisk (\*) indicates that key is for types only, and does not account for variation.

1. Setae on prolaeral coxa I hairlike, not basally swollen (Figs. 7, 8); small species ..... 2
- Setae on prolateral coxa spiniform, basally swollen (Figs. 9, 10)..... 4
- 2(1). Tarsus IV scopula partially divided by setae (Fig. 5)..... 3
- Tarsus IV scopula complete, not divided by setae (Fig. 6)..... *mojave* new species
- 3(2). Metatarsus IV scopula >30 distal percent and almost always <50% ..... *joshua* new species
- General reduction of metatarsal scopulation, metatarsus scopula <20%; Arizona. .... *paloma*
- 4(1). Metatarsus IV scopula < 35%; carapace and legs dark in color (Table 2) ..... *\*steindachneri*
- Metatarsus IV scopula  $\geq$  70%; carapace and patellae and tibiae I, II, pale buff (Table 2) ...
- ..... *iodium*

*Aphonopelma joshua* new species

Figs. 1, 2, 5, 7, 12-15, 22, 23, 51; Map 1.

**Types.**—Holotype male from San Bernardino County, allotype female from Riverside County, California, both from the Covington Flats area of Joshua Tree National Monument. Holotype collected at 10:09 PM, 6 September 1992, 2.3 mi. below the Covington Flats entrance to JTNM, elevation 3660 ft. Allotype excavated from a mounded burrow 21 October 1989, 5.6 mi. into the Monument in the Upper Covington Flat area, elevation 5140 ft. Paratype males (12): 24 July 1989 (1), 3 August 1989 (1), 10 August 1989 (2); 27–28 July 1990 (2); 27–28 July 1992 (5), 12 August 1992 (1). Paratype females (2): 3 May 1989 (1); 30 July 1992 (1). All paratypes collected by author in the Covington Flats area or near the JTNM entrance to this area. Types deposited in AMNH.

**Etymology.**—The specific name is a noun in apposition taken from the type locality, Joshua Tree National Monument.

**Diagnosis.**—*A. joshua* new species can be distinguished from all other species by the following combination of characters: small size, hair-like form of setae on prolateral coxa I (Fig. 7), partial division of tarsus IV scopula by setae (Fig. 5), and extent of metatarsus IV scopula. Males (Table 1) are most easily recognized by their unique coniciform setae of the sternum (Fig. 1), maxillae (similar to sternal setae), and coxae (Fig. 2) and the laterally swollen third femur (Fig. 13). They are separated from males of the most similar species, *A. mojave* new species, *A. radinum* and *A. paloma*, by the following: from *A. mojave* and

*A. radinum* by partial division of tarsus IV scopula (Fig. 5) and form of the palpal bulb (Figs. 14, 15) and from *A. paloma* by more extensive scopula of metatarsus IV (also III), respectively. Females (Table 2) are distinguished from those of all other species except *A. paloma* by partial division of tarsus IV scopula and from *A. paloma* by the more extensive scopula of metatarsus IV (all metatarsi).

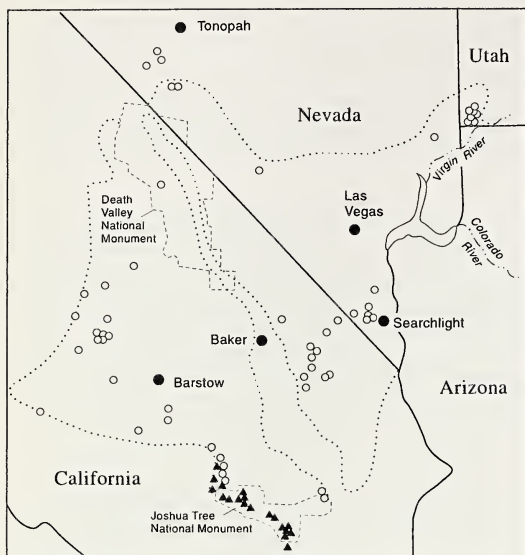
**Description.**—*Male:* Holotype. Overall length, 23.80; carapace, length, 8.80 width, 7.65; chelicerae, length, 2.80, width, 3.70. Cheliceral macroteeth, 8, denticles, 14 right, 15 left; sternum, length, 3.80, width, 3.60. Labial cuspules, 73; maxillary cuspules, 89 right, 98 left. Color of entire tarantula appears black; carapace pubescence black with a silver or gray-black sheen, appressed and moderately dense; chelicerae black with a silver sheen; abdominal pubescence gray-black, somewhat lighter than carapace. Abdominal anterodorsal setae black and relatively stout; lateral setae black, slender and shorter than dorsal setae; ventral setae black and finer than lateral setae; circular patch of dark black, type I (Cooke et al. 1972) urticating hairs (as in Fig. 11) covering posterodorsal half of abdomen, clearly visible; longest setae hairlike, pale orange-buff, basally dark, interspersed mostly within, just outside and caudally below urticating patch. Legs with black pubescence (legs appear gray-black), femora slightly darker; longest leg setae black with distal half pale orange-buff, other leg setae black. Ventral aspect black except red-orange labium and anterior palpal coxae and orange scopulae of palpal coxae. Cephalic region of carapace rising gradually



Table 2.—Females of *Aphonopelma*: Taxonomic characters and quantitative character values which separate the Mojave Desert *Aphonopelma* and *A. paloma*. °—species sharing the hairlike form of setae on prolateral coxa I, distinguished by superscript only from *A. joshua* (<sup>1</sup>) and *A. mojave* (<sup>2</sup>). \*—include in the synonymy of *A. iodium*; <sup>1</sup>—no overlap with *A. joshua*; <sup>2</sup>—no overlap with *A. mojave*; <sup>3</sup>—no overlap with *A. iodium*; gen dedu all—general reduction of all metatarsal scopulae; other abbreviations defined in Methods section of text. Mean and standard deviation shown in parentheses, i.e., (7.76, 1.34). Carapace measurements are in millimeters.

	<sup>°</sup> <i>joshua</i> [n = 10]	<sup>°</sup> <i>mojave</i> [n = 30]	<i>iodium</i> [n = 14]	<sup>°</sup> <i>paloma</i> [n = 11]	* <i>angusi</i> [allotype]
LC	6.00–9.70 (7.76, 1.34)	6.00–10.25 (8.03, 1.03)	<sup>21</sup> 10.80–22.05 (15.02, 2.65)	4.10–6.10 (5.05, 0.57)	<sup>3</sup> 9.10
LFI/LTI	1.26–1.32 (1.29, 0.02)	1.27–1.36 (1.31, 0.02)	1.32–1.38 (1.36, 0.02)	1.29–1.39 (1.35, 0.03)	1.32
LFI/LTII	1.44–1.50 (1.48, 0.02)	1.48–1.60 (1.54, 0.03)	1.50–1.57 (1.53, 0.02)	<sup>21</sup> 1.63–1.74 (1.68, 0.04)	<sup>1</sup> 1.56
LFI/LMI	1.41–1.55 (1.49, 0.05)	1.41–1.55 (1.48, 0.04)	1.29–1.47 (1.40, 0.04)	<sup>21</sup> 1.56–1.71 (1.64, 0.04)	<sup>3</sup> 1.52
LFI/LMII	1.40–1.57 (1.50, 0.06)	1.49–1.63 (1.55, 0.04)	1.33–1.52 (1.46, 0.05)	<sup>21</sup> 1.70–1.82 (1.76, 0.05)	<sup>3</sup> 1.56
LMIII/LMI	1.09–1.19 (1.15, 0.03)	0.99–1.10 (1.05, 0.03)	<sup>1</sup> 1.01–1.07 (1.04, 0.02)	<sup>1</sup> 1.00–1.07 (1.02, 0.30)	<sup>1</sup> 1.07
LAI/LC	2.26–2.43 (2.37, 0.06)	2.21–2.74 (2.39, 0.10)	2.23–2.51 (2.42, 0.09)	<sup>1</sup> 1.94–2.23 (2.13, 0.09)	2.39
LAIV/LC	2.59–2.84 (2.75, 0.07)	2.36–3.06 (2.63, 0.19)	2.41–2.70 (2.64, 0.11)	<sup>21</sup> 1.94–2.23 (2.13, 0.10)	2.68
LAI/LAIV	<sup>3</sup> 0.85–0.88 (0.86, 0.01)	<sup>1</sup> 0.89–0.94 (0.91, 0.01)	<sup>1</sup> 0.89–0.93 (0.92, 0.01)	0.88–0.94 (0.90, 0.02)	<sup>1</sup> 0.89
LAI/LAIII	1.08–1.15 (1.12, 0.02)	1.14–1.23 (1.18, 0.03)	1.11–1.15 (1.14, 0.01)	<sup>1</sup> 1.22–1.27 (1.25, 0.02)	<sup>31</sup> 1.16
Scopula MIV (%)	30–65 (40)	25–50 (35)	<sup>21</sup> 75–85 (lat) 45–60 (med)	<sup>21</sup> 0–17 gen redu all	<sup>21</sup> >70 (worn) 45 (med)
Division Sc TaIV (%)	<sup>2</sup> par div 40–70	<sup>1</sup> undivided	<sup>1</sup> undivided	<sup>2</sup> divided 40–67	<sup>1</sup> undivided
Prolateral CxI setae	hairlike bas uniform	hairlike bas uniform	<sup>21</sup> spiniform bas swollen	hairlike bas uniform	<sup>21</sup> spiniform bas swollen
Carapace color	black	black	<sup>21</sup> paper-bag brown	black	<sup>21</sup> paper-bag brown
Legs I, II, Palp (Ti, Pt color)	black	black	<sup>21</sup> paper-bag brown	black	<sup>21</sup> paper-bag brown

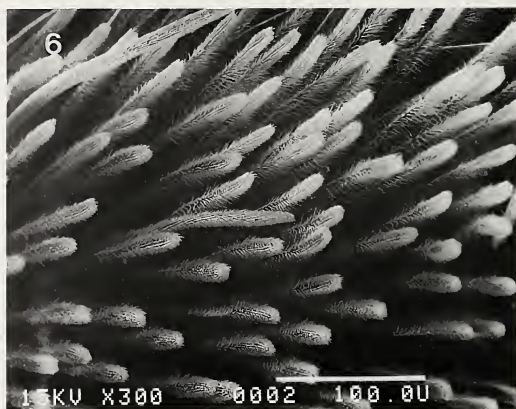
from thoracic groove, slightly less than twice the height of thoracic region. Ocular turret relatively high, compact, and steep resulting in a more lateral rather than dorsolateral inclination of lateral eyes, ocular area width 0.28× maximum width of cephalic region. AME circular; AME-AME, 0.6× AME diameter, AME-ALE, 0.15, 0.20× (left, right, respectively) AME diameter, AME-PME, 0.05, 0.10× AME diameter; ALE, PLE roughly ovoid (somewhat flattened ventrally), ALE length, 1.00× AME diameter, ALE-PLE, 0.20, 0.30× AME diameter, PLE, 0.90, 0.95× AME diameter, PLE-PME contiguous; PME ovoid, 0.70, 0.80× AME diameter. Thoracic groove a transverse pit with anterior border straight. Sternum widest between bases of coxae II & III; unique medial sternal setae short, basally swollen, and sharply constricted toward apex, some with hairlike apical portion but in most appear to be broken off;



Map 1.—Distribution of *Aphonopelma joshua* new species ( $\blacktriangle$ ) and *Aphonopelma mojave* ( $\circ$ ). The boundaries of the Mojave Desert (as perceived by the author) are indicated by the outer-most dotted lines; the area delimited by the inner-most dotted line indicates the geographic barrier that separates eastern and western populations of *A. mojave*.

marginal setae stout, slightly swollen basally, longer than medial setae; intermediate setae similar to marginal setae but less stout. Medial coxal setae (coxae I–IV) stout, thickened basally, similar to medial sternal setae although more elongate; distal and marginal setae similar to marginal sternal setae, proximal setae similar to intermediate and medial sternal setae. Distal maxillary setae similar to marginal sternal setae;

basomarginal, retromarginal, and medial setae similar to medial sternal setae but slightly less stout and usually apically filiform; most anterior setae relatively fine, hair-like. Femur III laterally swollen, at widest point 2.35, femur I, 1.70 (widest point other than at base just preapical of articulation with patella),  $WF_{III}/WF_I = 1.36$ . Prolateral face of coxa I with pad of fine hair-like, distally plumose setae both above and below suture. Tibia I arcuate, somewhat less than average condition. Leg and palp segment lengths in Table 3. Extent of scopulae ( $\times 100 =$  percent): metatarsi I & II complete; metatarsus III, prolaterodistal 0.75 (0.95 if scattered individual scopula hairs are considered), retrolaterodistal, left, 0.60, right, 0.55; metatarsus IV, 0.40 mediolateral. Metatarsus IV scopula completely divided by setae; tarsus IV scopula divided by setae proximal, left, 0.50, right, 0.60. Spination: metatarsus I, 1v(am), tibia I, L2d(1p0.30 1p0.70) R1d(1p0.30) L5v(1r0.10 1r 1r0.50 1p0.45 1p0.55) R3v(1er 1p0.50 1r0.55), femur I, 1d(p0.85); metatarsus II, L4v(1ap 1am 1ar 1r0.30) R2v(1am 1r0.35), tibia II, 2d(10.33 1p0.67) L4v(1ap 1ar 1r0.50 1r0.55) R5v(1ap 1ar 1p0.50 1r0.15 1r0.55), patella II, L1d(p0.50), femur II, 1d(p0.85); metatarsus III, 4d(1ep 1er 1p0.35 1r0.40) L6v(1ap 1am 2ar 1p0.45 1r0.20) R7v(1ap 1am 1ar 1p0.50 1r0.20 1r0.45), tibia III, L4d(1p0.25 1p0.65 1r0.15 1r0.90) R4d(1p0.60 1r0.20 1r0.60 1r0.90) L5v(2ap 1ar 1p0.50 1r0.50) R4v(1ap 1ar 1p0.50 1r0.45), femur III, R1d(1r0.80); metatarsus IV, L4d(1ep 1er 1p0.40 1r0.40) R3d(1ep 1er 1r0.45) L14v(1ap 1am 2ar 3p0.10–0.50 7r0.15–0.65) R14v(1ap 1am 1ar 2p0.30–0.50 8r0.10–0.80),



Figures 5, 6.—Tarsus IV scopulae. 5, *Aphonopelma joshua* new species, division of scopulae by setae (setae indicated by arrows); 6, *Aphonopelma mojave* new species, scopula undivided.

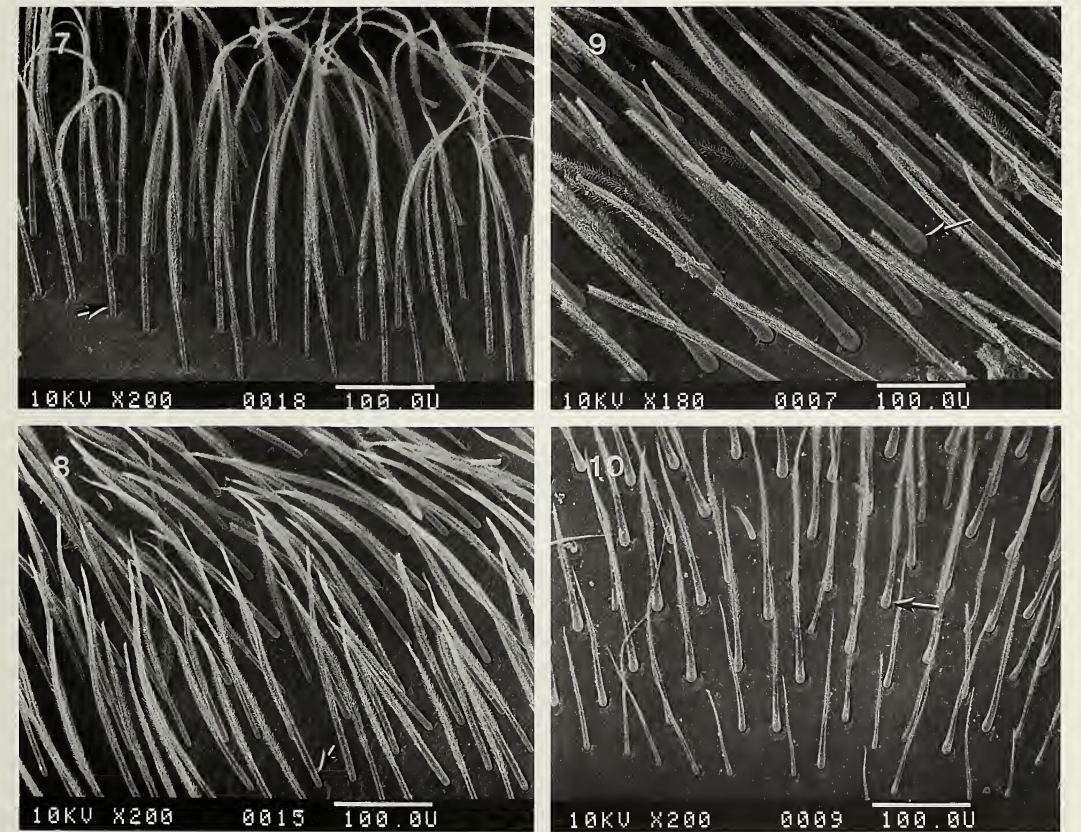


Table 3.—*Aphonopelma joshua* new species, holotype male: leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	9.20	8.75	8.40	9.80	5.20
Patella	4.25	3.90	3.60	3.80	2.80
Tibia	8.00	7.50	6.90	8.50	4.65
Metatarsus	8.20	8.30	9.60	11.75	
Tarsus	5.30	5.30	5.40	6.00	1.90
Total length	34.95	33.75	33.90	39.85	14.55

tibia IV, L1d(1r0.40) R3d(1p0.65 1r0.45 1r0.75) L5v(1ap 1ar 1p0.50 1r0.10 1r0.50) R4v(1ap 1ar 1p0.65 1r0.55); palpal tibia, 3d(1p0.35 1p0.60 1p0.85) L4v(1p0.55 1p0.80 1p0.85 1r0.50) R3v(1p0.55 1p0.80 1r0.45), palpal patella, L1d(p0.50), palpal femur, 1d(p0.85).  
*Female*: Allotype. Overall length, 28.0; carapace, length, 9.70, width, 8.70; sternum, length, 4.35, width, 4.00; chelicerae, length, 3.70,

width, 5.30. Cheliceral macroteeth, 7 right, 8 left; denticles, 9 right, 12 left. Labial cuspules, 50; maxillary cuspules, 72 right, 79 left. General color dark gray-black or black; carapace with bronze or gray-green sheen, pubescence appressed, medium density; chelicerae black with silver sheen; abdominal pubescence mouse gray or gray-black, oblong patch of urticating hairs black, clearly visible; legs gray, darker than abdomen, transitional between abdomen and carapace colors; ventral aspect dark gray-black (abdomen slightly less black) except orange color of labium, palpal coxae and scopulae of palpal coxae. Abdominal anterodorsal setae black, relatively long, with distal portion pale buff, less stout than homologous setae in male; long, basally dark pale orange-buff setae generally longer and slightly more slender than anterodorsal setae, interspersed mostly within and just outside of urticating patch; anterolateral, lower posterolateral, and ventral setae generally shorter



Figures 7–10.—Prolateral setae of coxa I (arrows indicate setal bases). 7, Hairlike setae of *Aphonopelma joshua* new species; 8, Hairlike setae of *Aphonopelma mojave* new species; 9, Spiniform, basally thickened setae, *Aphonopelma iodum*, Red Mountain, California; 10, Spiniform, basally thickened setae, *Aphonopelma iodum*, Beaver Dam Mountains, Utah.



and more slender than dorsal setae, similar in color to anterodorsal setae; dark ventral setae often very fine. Oblong patch of black urticating hairs covering posterodorsal 60% of abdomen. Legs with gray-black pubescence, shortest setae mostly black, longer setae with proximal half black, distal half pale orange-buff. Cephalic region of carapace rising from thoracic region at a steeper slope than in male, almost three times height of lowest area of thoracic region. Ocular turret intermediate in height, width  $0.24 \times$  maximum cephalic region width; lateral eyes with relatively normal dorsolateral orientation. AME circular, AME-AME,  $0.9 \times$  AME diameter, AME-ALE,  $0.4 \times$  AME diameter, AME-PME,  $0.15 \times$  AME diameter; ALE and PLE roughly ovoid, somewhat flattened ventrally; ALE length,  $1.0 \times$  AME diameter, ALE-PLE,  $0.5 \times$  AME diameter; PLE length,  $0.6, 0.7 \times$  AME diameter, PLE-PME almost contiguous; PME sub-circular,  $0.5 \times$  AME diameter. Thoracic groove transverse, slightly procurved. Sternum widest between bases of coxae II & III. Contrary to condition in male all sternal setae relatively fine and attenuate, medial setae generally longer but relatively slender compared to stout, spiniform marginal setae. Medial setae of coxae III & IV and most basal, promarginal, and retromarginal setae of all leg coxae intermediate between medial and marginal sternal setae in basal diameter; medial setae of coxae I & II similar to medial sternal setae. Basomarginal, retromarginal, and distal setae of palpal coxae intermediate in basal diameter, setae becoming more slender toward promargin. Femur III not swollen as in male. All leg segments shorter than carapace length; femur IV and metatarsus IV longer than femur I. Setation on prolateral face of coxa I as in holotype. Leg and palp segment lengths are in Table 4. Extent of scopulae ( $\times 100 = \%$ ): metatarsi I & II scopulae as in holotype; metatarsus III, prolaterodistal 0.60, retrolaterodistal 0.50; metatarsus IV, prolaterodistal 0.35, retrolaterodistal 0.25. Metatarsus IV scopula divided by setae; tarsus IV scopula divided by setae proximal 55 percent. Spination: metatarsus I, 1v(am), tibia I, L2d(1p0.25 1p0.60) (R2d(1p0.20 1p0.60) L5v(2ap 1ar 1p0.15 1p0.45) R5v(2ap 1ar 1p0.15 1p0.40), patella I, 1d(p0.50) R1v(m0.75), femur I, 1d(p0.80); metatarsus II, R1d(p0.35) 3v(1ap 1am 1r0.35), tibia II, L2d(1p0.25 1p0.60) L5v(2ap 1ar 1p0.15 1p0.45) R3d(1p0.20 1p0.60 1p0.85) R6v(2ap 1ar 1p0.35 1r0.15 1r0.40), patella II, 1d(p0.50)

Table 4.—*Aphonopelma joshua* new species, allotype female: leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	7.70	7.00	6.50	8.20	5.60
Patella	4.00	3.80	3.50	3.80	3.10
Tibia	5.90	5.20	4.70	6.40	4.20
Metatarsus	5.40	5.30	6.00	8.05	
Tarsus	4.00	4.00	4.20	4.70	4.00
Total length	27.00	25.30	24.90	31.15	16.90

1v(m0.85), femur II, 1d(p0.75); metatarsus III, L5d(1p0.15 1p0.35 1ep0.85 1r0.40 1er0.80) L6v(1ap 1am 1ar 1p0.25 1p0.40 1r0.40) R6d(1p0.15 1p0.45 1ep0.85 1r0.45 2er0.85) R5v(1ap 1am 2ar 1r0.40), tibia III, L6d(1p0.20 1p0.55 1p0.85 1r0.15 1r0.55 1r0.80) L6v(2ap 1ar 1p0.40 1r0.15 1r0.50) R5d(1p0.25 1p0.55 1r0.25 1r0.55 1r0.85) R10v(2ap 1ar 1p0.40 1p0.70 1r0.15 1r0.25 1r0.40 1r0.60 1r0.65), femur III, L2d(1r0.70 1r0.85) R2d(1p0.80 1r0.80); metatarsus IV, L4d(1p0.40 1ep0.90 1r0.45 1er0.90) L11v(1ap 1am 2ar 1p0.30 1p0.55 5r0.15–0.70) R4d(1p0.45 1ep0.85 1r0.40 1r0.90) R14v(1ap 1am 2ar 1p0.15 1p0.30 1p0.50 7r0.15–0.85), tibia IV, L4d)1p0.65 1r0.15 1r0.65 1r0.85) L7v(2ap 1ar 1p0.45 1r0.15 1r0.36 1r0.60) R4d(1p0.65 1r0.15 1r0.65 1r0.85) R6v(2ap 1ar 1p0.45 1r0.15 1r0.40), femur IV, L1d(r0.75); palpal tibia, 2d(1p0.55 1p0.90) L8v(3ap 1ar 1p0.25 1p0.60 1r0.45 1er0.85) R9v(2ap 1ar 1p0.25 1p0.60 1r0.20 1r0.45 1r0.60 1er0.90), palpal patella, 1d(p0.25), palpal femur, 1d(p0.85).

**Variation.**—*Males*: Total length 19.00–26.75. Cheliceral macroteeth, 7–9, 8 most common (60%), 9 least common (6%), denticles, 5–17. Labial cuspules, 33–78,  $\bar{x} = 54$ ; maxillary cuspules, 69–117 (each side),  $\bar{x} = 88$ . Coloration of new males tends to fade over time to dark brown-gray, carapace often with a bronze sheen. In some specimens the long pale orange-buff setae, normally interspersed within or just outside urticating patch, are sparsely interspersed on the venter, lateral surfaces, and slightly more anterior of urticating patch. Patch of type I urticating hair (as in Fig. 11) covering distal 40–60% of abdomen. Femur I and metatarsus III almost always longer than, rarely equal to or shorter than, carapace; tibia I usually shorter than, rarely equal to or longer than, metatarsus I; metatarsus I slightly to moderately arcuate



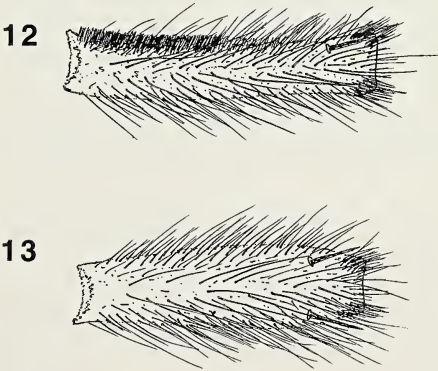
Table 5.—*Aphonopelma joshua* new species, males (25 including holotype): range of leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	7.85–9.85	7.40–9.40	7.20–9.00	8.35–10.50	4.30–5.60
Patella	3.60–4.50	3.40–4.20	3.00–3.80	3.20–4.00	2.30–2.90
Tibia	6.75–8.40	6.10–7.80	5.90–7.20	7.30–8.90	4.00–4.95
Metatarsus	6.85–9.00	6.80–9.20	8.10–10.55	10.20–12.70	
Tarsus	4.40–5.60	4.40–5.60	4.50–5.80	5.10–6.50	1.50–2.00

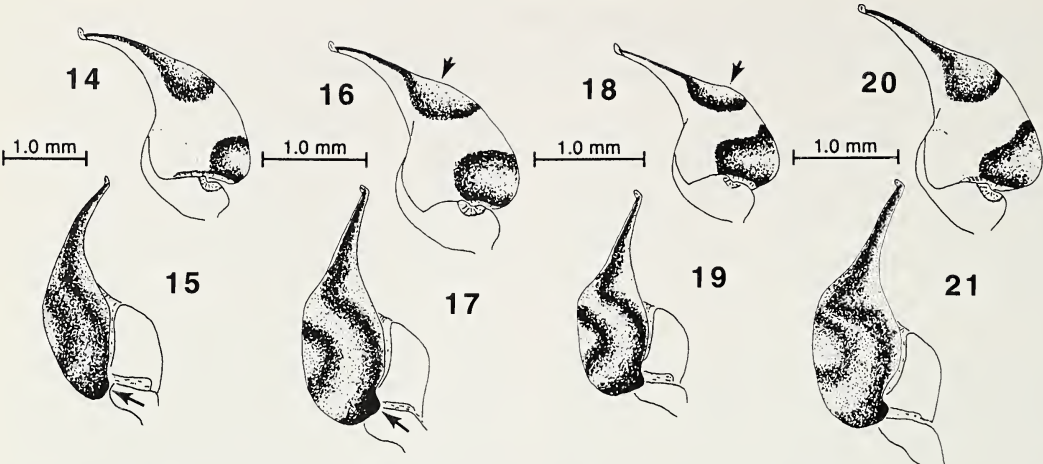
proximal portion of segment (in comparison to *A. mojave*); femur III laterally swollen (Figs. 12, 13), variable in degree. Ranges of leg and pedipalp segment lengths are in Table 5. Basal division of palpal bulb variable in shape; bulb itself and embolus (Fig. 14) relatively constant in shape; proximal prolateral protuberance of middle division slight (Fig. 15) or absent. Extent of scopulae ( $\times 100 = \%$ ): metatarsus II complete prolaterally but often very sparse or short of base retrolaterally and medially, metatarsus III prolaterodistal 0.50–0.85,  $\bar{x} = 0.63$  (often scattered hairs past 0.75), slight retrolateral reduction metatarsus IV 0.25–0.50,  $\bar{x} = 0.36$  (medial). Ventroapical metatarsal spination: I, 1–2, II, 2–3, III, 3–5 (usually 4), IV, 4–6 (usually 4).

*Females:* Total length 15.70–28.00. Cheliceral macroteeth, 7–9, 8 most common (70%), 9 least common (20%), denticles, 5–25 (each side). Labial cuspules, 50–97,  $\bar{x} = 69$ ; maxillary cuspules, 67–154 (each maxilla),  $\bar{x} = 93$ . Coloration of females tends to fade over time, carapace and chelicerae to bronze, gray-green, or brown-gray (chelicerae somewhat

darker), abdomen to mouse gray or faded carapace color (usually lighter), and legs to brown-gray (intermediate in color between carapace and abdomen) with femora and tarsi darker. In some females, the long, pale orange-buff abdominal setae are sparsely interspersed more anterior of the urticating patch, on the venter, and on the lateral abdominal surfaces. Spermathecae variable in shape and relative distance between bulbs (Figs. 22, 23). Although spermathecal characters have been found useful in distinguishing between other closely related mygalomorph species they appear to be of no diagnostic value in separating females of *A. joshua* from those of *A. mojave* (Figs. 24–28). Range of leg and pedipalp segment lengths in Table 6. Extent of scopulae ( $\times 100 = \%$ ): metatarsus III, prolaterodistal 0.55–0.85,  $\bar{x} = 0.65$  (only one specimen greater than 0.75), slight retrolateral reduction, metatarsus IV, distal 0.30–0.65 (usually medial),  $\bar{x} = 0.40$ , lateral extent slightly reduced, prolateral extent usually greater than retrolateral. Ventroapical metatarsal spination: I, 1–2, II, 2–3, III, 4–5 (rarely 5), IV, 4.



Figures 11–13.—11, Type I urticating hair, (*Aphonopelma mojave* new species, male, east Mojave); 12, 13, Femora of *Aphonopelma joshua* new species showing comparative widths; 12, Femur I (normal); 13, Femur III (swollen).



Figures 14–21.—Palpal bulbs of *Aphonopelma joshua* new species and *Aphonopelma mojave* new species, right; even, ventral (short arrows show retrolateral bend into apical portion); odd, dorsal (long arrows show position and degree of protrusion of proximal prolateral protuberance). 14, 15, *A. joshua*; 16, 17, *A. mojave*, east Mojave, near Kelso, California; 18, 19, *A. mojave*, east Mojave, BDM, Utah; 20, 21, *A. mojave*, west Mojave, Red Mountain, California.

**Distribution.**—*A. joshua* has a relatively limited distribution, primarily, in Joshua Tree National Monument between the northern flanks of the Eagle, Cottonwood and Little San Bernardino Mountains and the southern flanks of the Pinto Mountains (excluding the eastern Pinto Mountains and Pinto Basin), Queen Mountain, and Wonderland of Rocks. Outside of the monument, the species occurs south of the juncture of the Eagle and Cottonwood Mountains in a very limited area above 550 m in elevation, west of the northwestern boundary of the Monument in upper Morongo Valley, and north of Yucca Valley in two foothill desert valleys (San Bernardino Mountains), one serviced by Pipes Canyon Rd. (roughly parallels Pipes Wash), the other by New Dixie Mine Road, approximately 10 km north of Pipes Canyon Road, south of the Big-horn Mountains. This latter area appears to be the northern-most limit of the species. *A. josh-*

*ua* would be considered rare north of a diagonal connecting Queen Mountain and New Dixie Mine Rd. The distribution of *A. joshua* is shown on Map 1.

**Material examined.**—Type specimens and the following: **CALIFORNIA:** *Riverside County:* JTNM, Fried Liver Wash, 27 August 1965 (E.L.S. & S.L.J.), 1♀. Squaw Tank, 3500 ft. elev., 1♂, 9 September 1966 (E.L. Sleeper & S.L. Jenkins). Pleasant Valley, 1ma, 23 September 1967 (E.L. Sleeper & S.L. Jenkins). Lost Horse Valley, 1.1 mi. S of Quail Springs Rd. on Keys View Rd., 1 mi. W of K. V. Rd., 4383 ft. elev., definitive molt, 7 July 1989; 1♂, 3 May 1989. 4400 ft. elev., 1♀, Cottonwood Springs, near visitor's center, 3100 ft. elev., 3♂, 23 August 1989; Cottonwood Springs Rd, Smoke Tree Wash, 4.4 mi. N of visitor's center, 2710 ft. elev., 1♂, 31 August 1989. *San Bernardino County:* JTNM, west of Wonderland of Rocks, 4.5 mi. SE of monument entrance on Quail Springs Rd., 3950 ft. elev., definitive molt, 7 July 1989; 1♂, 28 March 1989; Pipes Canyon Rd. (Pipes Wash), 4.5

Table 6.—*Aphonopelma joshua* new species, females (10 including allotype): range of leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	4.90–7.70	4.40–7.00	4.00–6.50	5.15–8.20	3.60–5.60
Patella	2.60–4.00	2.40–3.80	2.20–3.50	2.40–3.80	2.00–3.10
Tibia	3.90–5.90	3.30–5.20	2.90–4.70	4.20–6.40	2.70–4.20
Metatarsus	3.20–5.40	3.15–5.30	3.60–6.00	5.10–8.05	
Tarsus	2.50–4.00	2.50–4.00	2.65–4.20	3.10–4.70	2.60–4.00



mi. W of Hwy 247, 4270 ft. elev., definitive molt, 24 June 1991; 1♂, 4 November 1989; 4300 ft. elev., 1♂, 1 August 1992; 2.5 mi. W of Hwy 247, 4000 ft. elev., definitive molt, July 1992; 1♂, 18 April 1990; 8.3 mi. W of Hwy 247 toward Burns Canyon, 4350 ft. elev., 3♀, 2 Nov. 1991; 5.9 mi. W of Hwy 247 toward Burns Canyon Rd., 4240 ft. elev., 1♀, 13 Sept. 1992; New Dixie Mine Rd., 10.5 mi. N Yucca Valley on Hwy 247, 6.3 mi. W, 5000 ft. elev., 1♀, 11 Sept. 1992; Morongo Valley, 5.1 mi. NE of Post Office off Hwy 62, 2890 ft. elev., 1♀, 6 Sept. 1993. Specimens collected by the author deposited in AMNH.

*Aphonopelma mojave* new species

Figs. 3, 4, 6, 8, 11, 16–21, 24–28; Map 1

**Types.**—Holotype male, allotype female, 9 paratype males, and 5 paratype females from San Bernardino County and Kern County California, south of Red Mtn., 20 mi. N of Kramer Jct. on Hwy 395, 1–2 mi. W of Hwy 395. Holotype collected 28 October 1989, 12:45 PM, 3450 ft. elev. Allotype lured out of burrow after dark 20 October 1991, 3250 ft. elev. Paratype males: 1974, 10 October 1989 (2) (W. Icenogle); 28 October 1991 (1); 14 October (1), 26 October (5), 2990–3450 ft. elev. Paratype females: 13 October 1991 (1), 20 October 1991 (1); 1992, 25 January 1992 (1), 4 October 1992 (1), 13 October 1992 (1), 3220–3280 ft. elev. All types except those specified collected by author. Types deposited in AMNH.

**Etymology.**—The specific name is a noun in apposition taken from the name of the desert within which the species appears to be almost totally contained.

**Diagnosis.**—*A. mojave* new species is distinguished from other species by the following combination of characters: carapace color, hair-like setae of prolateral coxa I (Fig. 8), undivided tarsus IV scopula (Fig. 6), limited extent of metatarsus IV scopula, and proportional lengths of tibiae and metatarsi I and II and leg III. In only three other species, *A. joshua*, *A. paloma*, and *A. radinum*, are the prolateral setae of coxa I hair-like. *A. mojave* is easily distinguished from the two former species by entire scopula of tarsus IV and again from *A. joshua* by the spiniform setae of the sternum (Fig. 3) and ventral coxae (Fig. 4) in males and from *A. radinum* (female unknown) by proportionately shorter tibiae I and II and longer leg III. In one other similar species, *A. marxi* (= *A. simulatum*), the prolateral

setae of coxa I are slightly swollen basally; *A. mojave* is distinguished from this species (females unknown) by proportionately much longer metatarsi I and II and legs III and IV. *A. mojave* is easily distinguished from two other small species, *A. phasmus* and *A. zionis*, by characters in Table 1.

**Description.**—**Male:** Holotype. Total length, 19.70; carapace, length, 8.50, width, 7.50; sternum, width, 3.65, length, 3.70; chelicerae, width, 3.80, length, 2.50. Cheliceral macroteeth, right 9, left 8; each side with 10 denticles. Labial cuspules, 33; maxillary cuspules, 90 right, 95 left. General color black with a faint bluish sheen; carapace with black pubescence, not appressed, moderately dense in cephalic region, increasing in density toward posterolateral and caudal margins. Abdomen clothed with blue-black pubescence; long, basally dark, orange-buff (or orange-tan) setae interspersed over entire dorsal, posterolateral, and caudal surfaces; slightly shorter versions of these setae on anterolateral and ventral surfaces, least dense on venter; circular patch of black type I urticating hairs (Fig. 11) covering posterodorsal 45 percent of abdomen, not clearly visible because of pubescence coloration and extensive interspersation of long orange-buff setae. Leg pubescence black, longer setae similar in color to abdominal setae, shorter setae dark with pale orangish-buff apices. Cephalic region rising gradually from thoracic region, slightly more than one and a half times higher. Ocular turret width slightly greater than 20 percent of maximum cephalic width, intermediate in height. AME circular, approximately 2.5, AME-AME,  $0.6 \times$  AME diameter, AME-ALE,  $0.15 \times$  AME diameter, AME-PME,  $0.1 \times$  AME diameter; ALE roughly ovoid, somewhat flattened ventrally,  $0.9 \times$  AME diameter, ALE-PLE,  $0.4 \times$  AME diameter, ALE-PME,  $0.5 \times$  AME diameter; PLE, subcircular,  $0.55 \times$  AME diameter, PLE-PME contiguous; PME irregular to elongate ovoid, slightly longer and narrower than PLE. Thoracic groove a transverse pit with anterior edge procurved. Medial sternal setae slender, attenuate; marginal setae basally stout, more spiniform; setae between medial and marginal setae intermediate in basal diameter. Promarginal and retromarginal setae of coxae I–IV similar in basal diameter to marginal sternal setae; medial setae similar to intermediate sternal setae. Baso- and retromarginal setae of palpal coxa similar to

Table 7.—*Aphonopelma mojave* new species, holotype male: leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	8.20	7.70	7.10	8.35	4.90
Patella	3.85	3.60	3.15	3.40	2.60
Tibia	6.60	5.95	5.30	6.85	4.50
Metatarsus	6.60	6.55	7.10	9.00	
Tarsus	4.50	4.50	4.50	5.00	2.00
Total length	29.75	28.30	27.15	32.60	14.00

intermediate sternal setae; distal setae similar to marginal sternal setae, setae becoming finer toward promargin of coxa. Femur III only slightly wider than femur I, WFIII/WFI = 1.09. Metatarsus I basally arcuate, bend moderate. Prolateral face of coxa I with fine, hairlike, distally plumose setae both above and below suture. Leg and palp segment lengths in Table 7. Extent of scopulae ( $\times 100 = \%$ ): metatarsi I and II to base (retrolateral scopula of metatarsus II, distal 0.85), metatarsus III, prolaterodistal 0.70, 0.75 (right and left, respectively), retrolaterodistal 0.55, 0.60, metatarsus IV, distal 0.40 medial, 0.25 lateral. Tarsus IV scopula entire, not divided by setae; metatarsus IV scopula divided proximal, right, 25, left, 40 percent. Spination: metatarsus I, 1v(am), tibia I, 2d(1p0.30 1p0.70) R4v(1br 1r0.20 1r0.50 1er) L4v(1br 1r0.50 2er), femur I, 1d(ep>0.80); metatarsus II, R3v(1r0.30 1ap 1am) L2v(1ap 1am), tibia II, 2d(1p0.25 1p0.65) R5v(1br 1r0.35 2ap 1ar) L5v(1br 1r0.50 2ap 1ar), femur II, 1d(ep>0.80); metatarsus III, R4d(1p0.35 1ep 1r0.40 1er) R5v(1p0.40 1r0.35 1ap 1am 1ar) L4d(1p0.45 1ep 1r0.40 1er) L5v(1p0.35 1r0.35 1ap 1am 1ar), tibia III, R4d(1p0.25 1p0.65 1r0.25 1r0.60) R3v(1r0.40 1ap 1ar) L3d(1p0.65 1r0.35 1r0.65) L4v(1p0.40 1r0.40 1ap 1ar), femur III, R1d(er); metatarsus IV, R3d(1r0.50 1ep 1er) R8v(1p0.15 1p0.50 1r0.15 1r0.50 1r0.60 1ap 1am 1ar) L4d(1p0.45 1r0.45 1ep 1er) L9v(1p0.30 1p0.50 1r0.15 1r0.45 1r0.55 1ap 1am 2ar), tibia IV, R1d(1r0.70) R4v(1p0.40 1r0.45 1ap 1ar) L3d(1r0.25 1r0.70 1r0.85) L3v(1r0.35 1ap 1ar); palpal tibia, R1d(p0.65) R3v(1p0.55 1p>0.80 1r0.40) L1d(p0.50) L3v(1p0.50 1p>0.80 1r0.45), palpal patella, 1d(p0.60), palpal femur, 1d(ep).

*Female*: Allotype. Total length, 26.40; carapace, length, 9.00, width, 7.75, LC/WC = 1.16; sternum, width, 4.05, length, 4.00; chelicerae, width, 4.80, length, 3.40. Cheliceral macroteeth,

8 each side, denticles, 19 right, 17 left. Maxillary cuspules, 101 right, 115 left; labial cuspules, 66. WCh/WC = 0.62. General color black, carapace with a blue-green-black sheen, pubescence moderately dense, not appressed. Black pubescence of abdomen with dull green cast, slightly darker than carapace. Long, basally dark, pale orange-buff setae interspersed over entire dorsum and posterolateral surfaces, anterodorsal setae with dark coloration extending further up shaft; anterolateral setae similar to anterodorsal setae. Most ventral setae short and black, longer ventral setae sparsely interspersed and similar to anterolateral setae. Patch of black, type I urticating hair covering posterodorsal half of abdomen, not clearly visible because of dark color of pubescence and extensive interspersation of long orange-buff setae. Legs with black pubescence similar in color to abdomen; shortest setae mostly black with distal portion pale tan, longer setae pale orange-buff with basal portion black. Cephalic region slightly higher and rising more abruptly from thoracic region than in male; thoracic groove transverse, anterior margin procurved; ocular turret occupying 23% of maximum cephalic width. AME circular, approximately 3.5, AME-AME, 0.9 $\times$  AME diameter, AME-ALE, 0.4 $\times$  AME diameter, AME-PME, 0.3 $\times$  AME diameter; ALE ovoid, somewhat flattened on bottom, length, 1.0 $\times$  AME diameter, ALE-PLE, 0.6, 0.75 $\times$  AME diameter; PLE, right irregular, length, 0.7 $\times$  AME diameter, left subcircular, 0.6 $\times$  AME diameter, PLE-PME, 0.1, 0.15 $\times$  AME diameter; PME elongate ovoid, length, 0.5 $\times$  AME diameter. Ventral setae of sternum as in holotype although homologous setae slightly less stout. Setae of ventral coxa and prolateral coxa I as in holotype. Femur III not swollen. Leg and palp segment lengths are in Table 8. Extent of scopulae ( $\times 100 = \%$ ): metatarsi I & II, to base (retrolateral scopula of metatarsus II, distal 0.80, medial scopula absent at very base); metatarsus III, left, prolaterodistal 0.85 (0.50 dense), retrolateral 0.70 (0.55 dense), right, prolaterodistal 0.80 (0.65 dense), retrolateral 0.55 (0.45 dense); metatarsus IV, left, distal 0.40 medial, 0.25 prolateral, 0.20 retrolateral, right, distal 0.40 medial, 0.30 prolateral, 0.20 retrolateral. Tarsus IV scopula entire, not divided by setae; metatarsus IV scopula, left, divided by setae proximal 40%, right, proximal 42 percent. Spination: metatarsus I, 1v(am), tibia I, 1d(p0.65) R5v(1r0.10 1r0.50 2ap 1ar) L4v(1r0.40 2ap 1ar), femur I,



Table 8.—*Aphonopelma mojave* new species, allotype female: leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	7.05	6.45	5.90	7.30	5.20
Patella	3.80	3.50	3.10	3.40	2.85
Tibia	5.50	4.75	4.20	5.75	3.85
Metatarsus	4.75	4.65	5.20	7.10	
Tarsus	3.70	3.60	3.60	4.00	3.60
Total length	24.80	22.95	22.00	27.55	15.50

1d(ep); metatarsus II, R1d(p0.35) L1d(p0.80) 3v(1r0.30 1ap 1am), tibia II, R2d(1p0.20 1p0.60) R5v(1r0.15 1r0.45 2ap 1ar) L2d(1p0.25 1p0.65) L3v(1r0.41 2ap 1ar), femur II, 1d(ep); metatarsus III, R3d(1r0.40 1ep 1er) L4d(1p0.35 1r0.40 1ep 1er) 5v(1p0.40 1r0.35 1ap 1am 1ar), tibia III, R3d(1p0.60 1r0.45 1r0.85) L5d(1p0.20 1p0.55 1r0.15 1r0.55 1r0.85) 6v(1p0.50 1r0.15 1r0.35 2ap 1ar), femur III, R1d(ep) L2d(1ep 1r0.60); metatarsus IV, 3d(1r0.45 1ep 1er) R8v(1p0.30 1p0.50 1r0.20 1r0.35 1r0.65 1ap 1am 1ar) L8v(1p0.50 1r0.15 1r0.25 1r0.40 1r0.50 1ap 1am 1ar), tibia IV, 3d(1r0.15 1r0.65 1r0.85) R6v(1r0.15 1r0.45 1r0.65 2ap 1ar) L5v(1p0.40 1r0.45 2ap 1ar), femur IV, L1d(er); palpal tibia, R2d(1p0.45 1p0.85) L2d(1p0.55 1p0.85) R8v(1p0.50 1p0.75 1r0.35 1r0.55 1er 2ap 1ar) L7v(1p0.20 1p0.55 1r0.40 1er 2ap 1ar), palpal femur, 1d(ep).

**Variation.**—*A. mojave* consists of an eastern and western race, geographically isolated from one another in the eastern and western Mojave Desert, respectively, by the Death Valley drainage. Eastern males have swollen third femora, and, although there is slight swelling in some western males there is no overlap in this character between the eastern and western races. The lower process of the tibial spur in eastern males is generally articulated at a lesser angle and is apically more angular or curved than in western males. The

smallest males of the species, found in Southern Utah, differ from other eastern males in having tibia I longer than metatarsus I instead of the usual reversed condition. While both conditions exist in western males there is quotient overlap only with eastern males from southern Utah. Eastern females have a relatively shorter metatarsus III than western females. In eastern specimens the carapace has a green-black or golden black (more common) sheen, the abdomen and chelicerae a green-black cast; in western specimens the carapace has black or blue-black sheen, the abdomen and chelicerae a blue-black cast.

**Males:** Total length, 15.1-21.1. Sternum length usually greater than but sometimes equal to width. Cheliceral macroteeth, eastern, 7-9, 7 most common (86%), 9 least common (2%), western, 6-9, 8 most common (55%), 7 (33%), 6 and 9 equally common (5%); denticles 4-20. Maxillary cuspules, western, 65-130 ( $\bar{x}$  = 101), eastern, 48-107 ( $\bar{x}$  = 82); labial cuspules, western, 33-90 ( $\bar{x}$  = 59), eastern, 26-68 ( $\bar{x}$  = 50). Long, pale orangish-buff setae of ventral abdomen may be sparse to moderately dense. Patch of type I urticating hairs covering distal 40-60% of abdominal dorsum. Tibia I arcuate, proximal bend moderate to strong, western males often with more pronounced bend. Ranges of leg and pedipalp segment lengths in Table 9. Little variation in morphology of the middle and apical portions of the palpal bulb (Figs. 16-21) and in form and articulation of basal division although significant variation in the shape of the basal division. ALE, PLE, and PME vary considerably in relative size, PLE and PME in shape also; AME circular, most consistently shaped, AME-AME less than their diameter apart; ALE generally ovoid with ventral perimeter of eye somewhat flattened, in western specimens length usually equal to or slightly less than, seldom greater than AME diameter, in eastern

Table 9.—*Aphonopelma mojave* new species, males (42 including holotype): range of leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	6.40-9.35	6.00-8.80	5.55-8.10	6.40-9.60	3.75-5.60
Patella	2.95-4.45	2.80-4.20	2.50-3.70	2.70-3.95	2.10-3.05
Tibia	5.35-7.65	4.85-6.95	4.25-6.10	5.60-7.85	3.60-5.25
Metatarsus	5.25-7.70	5.30-7.65	5.75-8.40	7.15-10.50	
Tarsus	3.70-5.10	3.60-5.10	3.50-5.20	3.80-5.80	1.60-2.40

Table 10.—*Aphonopelma mojave* new species, females (30 including allotype): range of leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	4.55–7.85	4.00–7.20	3.55–6.65	4.55–8.15	3.35–5.75
Patella	2.55–4.60	2.30–3.90	1.95–3.35	2.30–3.65	1.90–3.05
Tibia	3.45–5.85	2.90–5.15	2.45–4.50	3.70–6.30	2.35–4.05
Metatarsus	2.95–5.30	2.80–5.20	3.00–5.70	4.15–7.85	
Tarsus	2.40–4.00	2.30–4.00	2.30–4.10	2.60–4.50	2.30–4.00

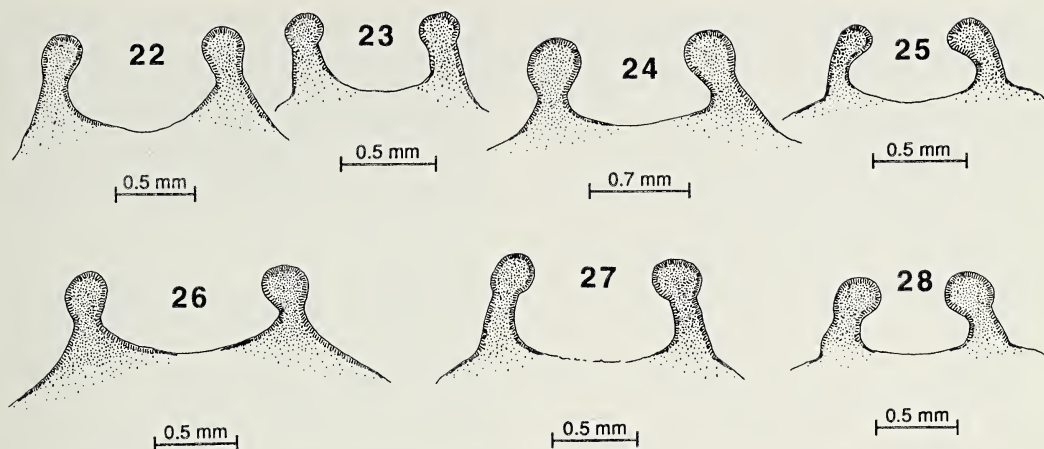
specimens length usually greater than, seldom less than AME diameter; PLE usually smaller than ALE and larger than PME, usually ovoid, sometimes subcircular or irregular, PLE-PME barely removed or contiguous; PME often elongate ovoid or irregular, sometimes subcircular, generally smaller than PLE. Extent of scopulae ( $\times 100 = \%$ ): retrolateral scopula of metatarsus II often short of base; metatarsus III, western, distal 0.60–0.85, eastern, 0.55–0.85 (prolateral maximum); metatarsus IV, western, distal 0.30–0.45,  $\bar{x} = 0.39$ , eastern, 0.25–0.55 (medial usually maximum),  $\bar{x} = 0.33$ . Metatarsus IV scopula entire to divided, western, proximal 71%, eastern, proximal 86%. Ventroapical metatarsal spination: I, 1, II, 1–3 (usually 2), III, 2–6 (eastern, usually 4, western, usually 3), IV, 3–8 (eastern, usually 4 or 5, western, usually 4).

*Females*: Total length, 14.6–24.1. Sternum widest between coxae I and II; width greater than (in more than 50% of specimens),  $\leq$  length in western race; width less than length in eastern race. Cheliceral macroteeth, west, 7–9, 8 most common (63%), 9 least common, east 6–9, 7 most common (57%), 8 (33%), 9 least common. Maxillary cuspules each side, western, 79–149 ( $\bar{x} = 111$ ), eastern, 58–114 ( $\bar{x} = 83$ ); labial cuspules, western, 35–100 ( $\bar{x} = 74$ ), eastern, 26–85 ( $\bar{x} = 54$ ). Carapace pubescence usually not closely appressed although frequently more appressed than in males. Long orangish-buff abdominal setae varies in density, often more sparse ventrally than in males. Patch of type I urticating hairs covering distal 40–70% of abdominal dorsum. Ranges of leg and pedipalp segment lengths in Table 10. Spermathecae variable in both shape and distance between spermathecal bulbs (Figs. 24–28), variation not correlated with geography. Eye arrangement as in male, posterior eyes most variable in relative size and shape, AME least variable; distance be-

tween adjacent eyes variable. Extent of scopulae ( $\times 100 = \%$ ): metatarsi I and II as in allotype, metatarsus III, distal 0.55–0.85, western,  $\bar{x} = 0.73$ , eastern,  $\bar{x} = 0.62$ , metatarsus IV, distal 0.25–0.50 (western  $\bar{x} = 0.38$ , eastern  $\bar{x} = 0.32$ ). Tarsus IV scopula entire, not divided by setae; metatarsus IV scopula usually partially divided by setae, less often, entire or completely divided. Ventroapical metatarsal spination: I, 1–2 (eastern, 1 or 2, western, usually 1) II, 1–3 (usually 2), III, 2–6 (eastern, usually 4, western, usually 3), IV, 3–6 (eastern, most often 4, less often 5, western, most often 4, less often 3).

**Distribution.**—*A. mojave* is found throughout the Mojave Desert except in certain regions of south-central Nevada, areas that geographically isolate the eastern and western races and BDM populations from other eastern populations, and most of JTNM. Only the northern-most populations near Goldfield Summit (western Nevada) inhabit biomes not characteristic of the Mojave Desert. East of Goldfield Summit toward the Beaver Dam Mountains, populations may exist in some of the less rocky valleys between the southern Nevada north-south mountain ranges although I am unaware of specimens collected in these areas. The Virgin Mountains, the rugged terrain toward the Grand Canyon, and decreasing elevations toward the Colorado River apparently bound the distribution of the eastern race. The (apparently) isolated populations of southern Utah and adjacent Arizona and Nevada were found as far south as the southern bajadas of the Mormon Mountains. The only known population in JTNM barely extends across the Monument's boundary in the extreme northeastern corner, just west of the Coxcomb Mountains where Pinto Basin exceeds 550 m elevation. *A. mojave* is considered rare in the southwestern Mojave south of the diagonal from Queen Mountain (JTNM)





Figures 22–28.—Spermathecae of *Aphonopelma joshua* new species and *Aphonopelma mojave* new species. 22, 23, *A. joshua*, JTNM; 22, Covington Flats; 23, Fried Liver Wash, Pleasant Valley; 24, 25, *A. mojave*, west Mojave, Red Mountain, California; 26, *A. mojave*, west Mojave, NE Coxcomb Mountains, JTNM; 27, *A. mojave*, west Mojave, Yucca Valley, La Contenta Rd.; 28, *A. mojave*, east Mojave, Searchlight, Nevada.

to Pipes Canyon (foothills of the San Bernardino Mountains). The distribution of the species is shown on Map 1.

**Material examined.**—Type specimens and the following: **CALIFORNIA:** *San Bernardino County:* Halloran Summit, 0.5 mi. NW of I-15, 4125 ft. elev., 1♀, 24 September 1989. Hwy 247, Rattlesnake Springs Rd. W of Johnson Valley, 3140 ft. elev., 1♀, 1 November 1989. Apple Valley, S of A. V. toward Rattlesnake Mtn., 4060 ft. elev., 1♀, 4 November 1989. NE JTNM inside and outside of monument boundary, just west of Coxcomb Mtns. off Hwy 62, 12.2 mi. W of jct. Hwy 177, 2320 ft. elev., 1♀, 12 November 1989; 2050–2130 ft. elev., 3♂, 24 November 1989; 2050 ft. elev., 1♀, 31 January 1991; 2300 ft. elev., 1♀, 2 November 1991. Honda Rd., N of Yucca Valley off Hwy 247, 3890 ft. elev., 1♀, 14 April 1990; 3870 ft. elev., 1♀, 14 April 1991. Hwy 247, 20 mi. S of Barstow, 3200 ft. elev., 2♂, 16 October 1990 (S. Kutcher); 1♂, 26 October 1991. 7.5 mi. N of Pipes Canyon Rd. (Pipes Wash), 3680 ft. elev., definitive molt, late September–early October 1991; 1♂, 14 April 1991. 3.7 mi. N of Pipes Canyon Rd., 3400 ft. elev., 1♀, 18 April 1991. E of Yucca Valley, La Contenta Rd. between Hwy 62 and Yucca Trail Rd., 3275 ft. elev., 1♀, 2 November 1991. Apple Valley, 2 mi. S on Milpas Dr. off Hwy 78, 3040 ft. elev., 1♀, 5 May 1992. Cima, N of Cima, 4.6 mi. W on power line road, 4350 ft. elev., 1♂, 10 October 1992. 2.9 mi. W on power line road, 4590 ft. elev., 2♀, 11 October 1992. Black Canyon Rd., 2.8 mi. N of Essex Rd. jct., 3240 ft. elev., 1♀, 11 October 1992; 1♀, 25 October 1992. Kelbaker Rd., 9.4 mi. S of Kelso, 3120 ft. elev., 1♂, 31 October 1992. Cima,

1.5 mi. W of Kelso-Cima Rd. W of Cedar Canyon Rd., 3800 ft. elev., 1♂, 31 October 1992. Kelbaker Rd., 8 mi. S of Kelso, 2880 ft. elev., 1♂, 1 November 1992. Kelso-Cima Rd., 10 mi. N of Kelso, 3300 ft. elev., 1♂, 1 November 1992. Morning Star Mine Rd., 3.1 mi. SW of Ivanpah Rd. 3005 ft. elev., 1♂, 1 November 1992. Nipton, between Nipton and Nevada state line, 3245 ft., 3705 ft. elev., 2♂, 1 November 1992. **Kern County:** Hwy 395, 8.1 mi. N into Kern Co., 3500 ft. elev., 1♂, 20 October 1991. **Inyo County:** Death Valley National Monument, jct. Harrisburg Flats, Skidoo Rd., 5000 ft. elev., 2♂, 18 October 1963 (R. Hardy). **Los Angeles County:** San Gabriel Mtns. foothills, north slope off N2, 1♂, 21 October 1976 (M.E. Thompson). Canyon Country, N on Hwy 14, 1♂, 30 October 1978 (M. Wilkerson). Valyermo, Bob's Gap Rd., 1.5 mi. N of N4, 4050 ft. elev., 1♂, 28 October 1989. **NEVADA:** **Clark County:** Searchlight, 0.5–3.0 mi. W of SL., 3300 ft. elev., 4♂, 23 October 1976 (W. Icenogle). 8.2 mi. W of SL., 0.5–1.5 mi. N of Hwy 164, 4280 ft. elev., 2♀, 7 October 1989; 4365 ft. elev., 1♀, 12 October 1990; 4180–4260 ft. elev., 3♀, 12 October 1991. **Nye County:** 10 mi. W of Mercury, 2♂, 3 November 1972 (W. Icenogle). Scotty's Jct., 10 mi. S on Hwy 95, 4000 ft. elev., 2♂, 28 October 1978 (W. Icenogle). Lida (Hwys 266 and 95 jct.), 5.5 mi. S, 4500 ft. elev., 1♂, 28 October 1978 (W. Icenogle). **Esmeralda County:** Goldfield Summit, 8 mi. S on Hwy 95, 5000 ft. elev., 1♂, 28 October 1978 (W. Icenogle). **UTAH:** **Washington County:** Beaver Dam Mtns., Summit Springs off old Hwy 91, 4140 ft. elev., 1♀, 6 October 1993; 3960–4120 ft. elev., 3♀, 12 October 1993. Old Hwy 91, 2.7–3.5 mi. N of Utah-Arizona line, 3140–3300 ft. elev.,



Map 2.—Distribution of *Aphonopelma iodium*. The boundaries of the Mojave Desert (as perceived by the author) are indicated by the outer-most dotted lines.

4♂, 19–20 October 1993. W of Hwy 91, 2.4 mi. W of Welcome Springs Rd. turnoff, 3680 ft. elev., 1♂. Specimens collected by the author deposited in AMNH.

*Aphonopelma iodium* (Chamberlin & Ivie)

Figs. 9, 10, 29–50; Map 2

*Delopelma iodius* Chamberlin & Ivie 1939: fig. 3 (male holotype from Washington County, Utah, 2 miles west of Castle Cliffs (Beaver Dam Mountains), 27 November 1936, in AMNH, examined).

*Aphonopelma iodius*: Chamberlin 1940: 7.

*Aphonopelma iodium*: Smith 1994: 115. Spelling change, gender neuter.

*Delopelma melanius* Chamberlin & Ivie 1939: fig. 1 (male holotype from Salt Lake County, Utah, University of Utah campus, September 1925, in AMNH, examined; female allotype lost).

*Aphonopelma melanius*: Chamberlin 1940: 6. NEW SYNONYMY.

*Aphonopelma melanium*: Smith 1994: 120. Spelling change, gender neuter.

*Aphonopelma nevadanum* Chamberlin 1940: 13 (male holotype from Clark County, Nevada, collected by G. Carter, searchlight, 2 December

1930, in AMNH, examined). NEW SYNONYMY.

*Aphonopelma angusi* Chamberlin 1940: 21–22 (male holotype and female allotype from Washington County, Utah, collected by A.M. Woodbury, R. Hardy, H. Higgins, and R. Pendleton, 2 miles west of Beaver Dam Mountains, 7 October 1939, in AMNH, examined). NEW SYNONYMY.

**Synonymy.**—*Aphonopelma melanium*, *A. angusi*, and *A. nevadanum* are placed in the synonymy of *A. iodium* (one of two possible senior synonyms) with which they share all characters of specific significance (Tables 1, 2); there are no other characters known that merit their continued separation. The *A. angusi* allotype has a shorter carapace (carapace length 9.10) than any other conspecific female examined in this study; the ratio of its carapace length to that of a larger female from the type locality is 0.64. However, corresponding ratios of the smallest to largest females in *A. joshua* and *A. mojave* and males in *A. iodium* are 0.64, 0.59, and 0.66, respectively (smallest and largest of each species from the same locality). Metatarsi I and II are proportionately shorter relative to femur I in the *A. angusi* allotype than in other *A. iodium* females. Although no other correlation between the size and proportional leg or leg segment length was found within the combined sample, the proportionately shortest metatarsi I and II (excluding *A. angusi* allotype female) were found in the smallest female (carapace length 10.80) and the proportionately longest metatarsi in the largest female (carapace length 22.05). Therefore, both carapace and relative metatarsal lengths in the allotype are believed to be extensions of the female range for these characters. Leg and pedipalp segment lengths of the *A. angusi* allotype are in Table 13. All ‘*eutylenum* type’ tarantulas of the Mojave Desert are considered *A. iodium*, sharing with the type all specifically significant characters. Ecological, behavioral, and distribution data gathered from this assemblage support the synonymy of *A. iodium*.

**Diagnosis.**—*Aphonopelma iodium* is easily distinguished from *A. joshua*, *A. mojave*, and *A. steindachneri* by extensive scopula of metatarsus IV and by the pale-buff color of the carapace and of the patella and tibiae of legs I and II in females. There are only two valid species (‘*eutylenum* types’?) described



prior to 1939, *A. rusticum* (Simon) and *A. helluo* (Simon), in which the carapace coloration (as described) and extent of metatarsus IV scopula are similar to the corresponding characters in *A. iodium* (ambiguity in proper type representation of *A. rusticum* is discussed in the 'Status of some old *Eurypelma* species' subsection above). *A. iodium* is distinguished from *A. rusticum* (USNM, cotype #1585) by longer legs relative to carapace length (Table 1); although most segments of leg I of the cotype are missing,  $LFI/LC = 0.88$ ; in *A. iodium*  $LFI/LC = 0.93$ – $1.07$ . The *A. rusticum* paratype specimen (MNHP-Paris, #5873), considered the lectotype by Smith, is doubtfully of the same species as the USNM cotype specimen since the length of the patella plus tibia IV (also patella plus tibia I) is less than the length of the carapace in the former ( $LP + TIV/LC < 1.00$ ) and greater than the carapace length in the latter ( $LP + TIV/LC = 1.11$ ); in *A. iodium* males  $LP + TIV/LC = 1.18$ – $1.32$  which clearly distinguishes it from both specimens. Proportionately longer legs in *A. iodium* males further distinguishes the species from that of the Mazatlan paratype male. Based on Simon's locality data, I believe that *A. rusticum* is most likely a summer breeder. *A. iodium* is distinguished from *A. helluo* (holotype male #17707 and non-type male #50(44)) by a shorter carapace and longer legs relative to carapace length and again from the non-type male by more extensive scopulae of metatarsi III and IV and proportionately longer metatarsi I and II (measurements of the holotype were taken from Smith; numerical and character data from the non-type male are in Table 1). Other species in the '*eutylenum* group' include *A. eutylenum*, *A. clarum*, *A. brunnium* (*brunnius*), *A. cryptethum* (*cryptethus*), *A. cratium* (*cratius*), *A. prosoicum* (*prosoicus*), and *A. griseum*. Although *A. iodium* can be distinguished from all of these types by various leg and palpal length proportions (or segment proportions), the character differences in the types of *A. eutylenum*, *A. clarum*, *A. brunnium*, *A. cryptethum*, and *A. cratium* appear to be minimal. Consequently, the unambiguous separation of *A. iodium* from any of the five species will remain questionable until the variational limits of these quantitative characters have been determined for various populations of inland and coastal '*eutylenum* types'.

**Description.**—*Males*: Carapace, length 9.35–16.90 ( $\bar{x} = 13.0$ ), width 8.10–15.60; smallest males found in southern Utah. Sternum, length 4.20–7.60, width 3.80–6.85; usually longer than wide, length equal to width in one male from JTNM. Chelicerae, width 4.20–7.95. Cheliceral macroteeth 7–9, denticles 4–16. Labial cuspules 55–140 ( $\bar{x} = 102$ ); maxillary cuspules 103–234 (each side) ( $\bar{x} = 181$ ). Color of carapace pubescence pale buff or paper-bag brown (usually darker with greenish-bronze sheen following molt, most pronounced in cephalic region); black to dark brown abdomen and appendages; chelicerae similar in color to carapace but usually slightly darker. Patch of black type I urticating hairs covering posterodorsal 45–65% of abdomen, difficult to distinguish because of pubescence coloration and interspersions of long orange-tan setae. Abdominal anterodorsal setae spiniform, stout, and uniformly black or dark reddish-brown; anterolateral setae also dark but shorter and more slender than dorsal setae; longest setae filiform, orange-tan with dark basal portions, interspersed on posterodorsal, posterolateral, and caudal surfaces, the longest inside and just outside of patch of urticating hair, the shortest toward ventral margins; abdominal venter usually with sparse interspersions of similar setae and a dense covering of short, fine, dark setae. Sternum with relatively slender, attenuate medial setae and more stout, spiniform marginal setae; setae intermediate in position also intermediate in basal diameter. Coxae (I–IV) with retromarginal, promarginal, and distal setae similar to marginal sternal setae; most basomarginal and medial setae similar to intermediate and medial setae of sternum. Baso- and retromarginal setae of palpal coxae similar to medial or intermediate sternal setae. Sternal and ventral setae of coxae very similar to, if not indistinguishable from, homologous setae of *A. mojave* males (Figs. 3, 4, respectively). Setae on prolateral surface of coxa I spiniform and basally swollen (Figs. 9, 10). Leg setae attenuate, mostly pale buff with dark basal portion, the shortest mostly dark with pale distal ends. Metatarsus IV almost always longer than length of carapace, rarely equal to and always longer than femur I; metatarsus I generally longer than tibia I but can be slightly shorter than tibia I in males from southern Utah. Leg and pedipalp segment lengths of the holotype are in Table 11;

Table 11.—*Aphonopelma iodium*, holotype male: leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	15.40	14.60	13.35	15.20	9.15
Patella	7.10	6.60	5.80	6.20	4.75
Tibia	12.60	11.55	9.90	12.40	8.30
Metatarsus	13.35	13.00	13.60	16.90	
Tarsus	8.10	7.90	7.60	8.40	3.30
Total length	56.55	53.65	50.25	59.10	25.50

ranges of segment lengths in Table 12. Retro-lateral bend into apical division of the palpal bulb uniform rather than abrupt and bulb relatively slender (Figs. 29, 31, 33, 35, 37, 39, 41, 43) compared to bulb of *A. mojave*; proximal prolateral protuberance on the dorsal aspect prominent (Figs. 30, 32, 34, 36, 38, 40, 42, 44) as in *A. mojave* males. Extent of scopulae ( $\times 100 = \%$ ): metatarsi I and II to base, metatarsus III, prolateral, usually to base or near to base, medial, 0.60–0.80, metatarsus IV, retrolateral, distal 0.70–0.85, medial, 0.40–0.55. Tarsal scopulae entire, not divided by setae. Ventroapical metatarsal spination: I, 1–3 (usually 2), II, 1–4 (usually 3), III, 2–5 (often 4, less often 3), IV, 2–5 (almost always 4).

*Females*: Carapace, length, 10.80–22.05 ( $\bar{x} = 15.02$ ), width, 9.65–18.70. Sternum, length, 4.60–8.70, width, 4.70–7.80, usually longer than wide but slightly wider than long in smallest female. Chelicerae, width, 6.25–12.65. Cheliceral macroteeth, 7–10, denticles, 7–15 ( $\bar{x} = 11$ ). Labial cuspules, 100–138 ( $\bar{x} = 114$ ); maxillary cuspules 129–267 (each side),  $\bar{x} = 195$ . Color of carapace and chelicerae as in males; color of tibiae and patellae of legs I, II, and palps similar to carapace (color varying in degree), corresponding segments of legs III & IV less accentuated but usually slightly lighter than the remaining leg segments. Patch of black type I urticating hairs covering posterior  $\frac{1}{2}$ – $\frac{3}{4}$  of abdominal dorsum.

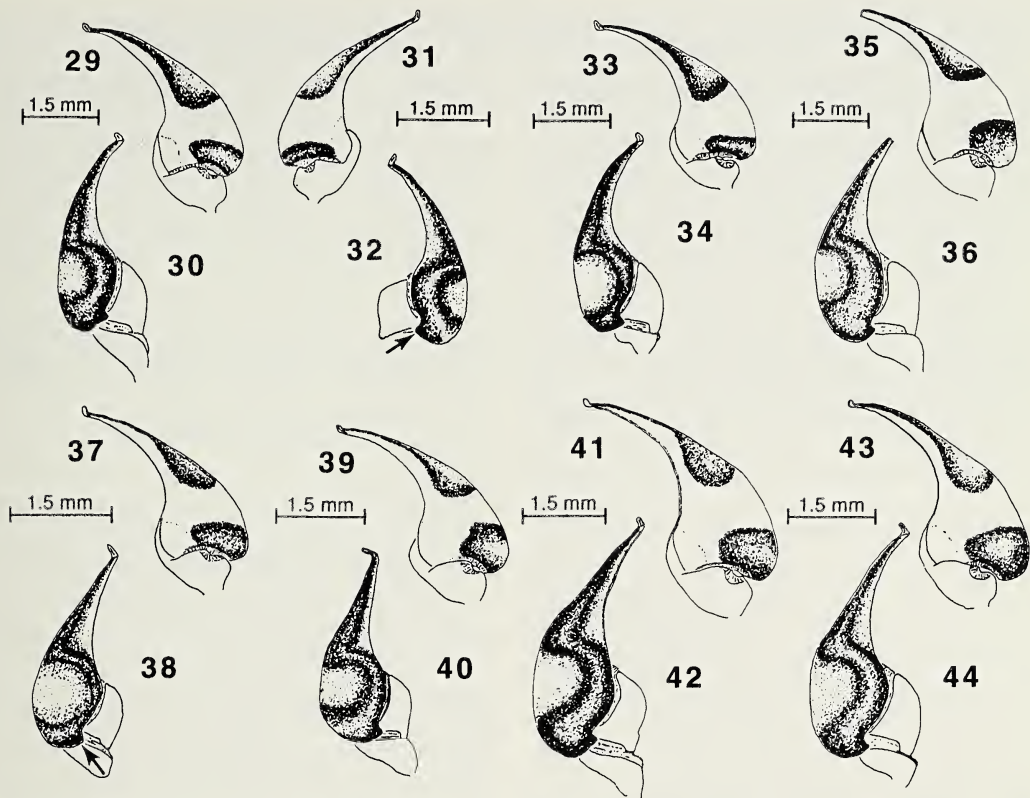
Abdominal anterodorsal setae similar to those of males but less stout and distally pale buff; longest setae basally dark, orange-tan, distributed as in males relative to patch of urticating hair but often dispersed further anteriad. Sternal, coxal, and leg setae as in males although homologous setae often slightly less stout. Metatarsus IV and femur I always shorter than length of carapace; metatarsus I usually shorter than tibia I but longer than in largest female (JTNM); femur IV longer than femur I; metatarsus III longer than metatarsus I. Ranges of leg and palpal segment lengths are in Table 14. Variations in the shape of spermathecae and relative distance between bulbs (Figs. 45–50) are inconsistent with population geography (it is not currently known if spermathecal characters adequately distinguish any *Aphonopelma* species). Extent of scopulae ( $\times 100 = \%$ ): metatarsi I and II, to base, metatarsus III, lateral, to base or close to base, medial, distal 0.70–0.80, metatarsus IV, retrolateral, 0.75–0.85, medial, 0.50–0.60. Tarsal scopulae entire, not divided by setae. Ventroapical metatarsal spination: I, 1–3 (usually 2), II, 1–3 (often 3, less often 2), III, 3–4 (equally common), IV, 4.

**Distribution.**—*A. iodium* is common throughout the Mojave Desert west of the Colorado River, its distribution continuous to the north into the Great Basin in Utah and Nevada. Its distribution to the south and to the west of the Mojave Desert and to the northern-most limits in Nevada and Utah has not yet been determined. However, preliminary data from extensive fieldwork suggest that to the south (excluding the low desert) and west *A. iodium* is replaced by an inland and coastal species (*'eutylenum* type') while to the north it is the only theraphosid species, other than *A. mojave*, found in Nevada and the only *'eutylenum* type' found in Utah. The known distribution of the species within the Mojave Desert is shown on Map 2.

Table 12.—*Aphonopelma iodium*, males (32): range of leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	9.70–17.55	9.20–16.80	8.50–15.50	9.65–17.70	6.00–10.45
Patella	4.70–8.25	4.25–7.60	3.70–6.85	3.95–7.20	3.30–5.50
Tibia	8.15–13.75	7.15–12.90	6.15–11.45	7.85–13.80	5.40–9.95
Metatarsus	8.15–16.10	8.10–15.75	8.45–16.35	10.75–20.60	
Tarsus	5.30–9.30	5.10–8.80	5.00–8.80	5.70–9.70	2.45–3.80





Figures 29–44.—Palpal bulbs of *Aphonopelma iodium*, right; odd, ventral; even, dorsal (arrow-proximal prolateral protuberance). 29, 30, Holotype, *A. iodium*; 31, 32, Holotype, *A. angusi* (left bulb); 33, 34, Holotype, *A. melanium*; 35, 36, Holotype, *A. nevadanum* (tip of embolus broken); 37–44, Mojave Desert; 37, 38, Mojave Desert, BDM, Utah; 39, 40, Mojave Desert, Searchlight, Nevada; 41, 42, Mojave Desert, Quail Mountain, JTNM; 43, 44, Mojave Desert, Red Mountain, California.

**Specimens examined.**—Holotype male, holotypes: *A. melanium*, *A. angusi*, and *A. nevadanum*, allotype: *A. angusi*, and the following: **CALIFORNIA: Riverside County:** JTNM: Cottonwood Springs, 3000 ft. elev., definitive molt, 21–22 September 1986; 1♂, 25 February 1985. 1.0–1.5 mi. E of Cottonwood Springs, 3300 ft. elev., 1♀, 4 April 1989. Hexie Mtns. W of Cholla Cactus Gardens on Pinto Basin Rd., 2760 ft. elev., 1♀, 16 April 1989. Quail Mtn., 5.7 mi. SE of monument entrance off

Quail Mtn. Rd., 0.5 mi. SW of picnic area, 4080 ft. elev., 1♀, 5 August 1989. **San Bernardino Co.:** Reche Rd., 4.5 mi. E of Landers, 2950 ft. elev., 1♂, 18 October 1981 (W. Icenogle). NE Coxcomb Mtns., 8 mi. W of jct. Hwy. 177 on Hwy 62, 1600 ft. elev., 2♀, 4 February 1990. East Mojave, Mid Hills toward campground, 5700 ft. elev., definitive molt, 2 August 1989; 1♂, 13 May 1989. **JTNM:** Quail Springs Rd., 2.7 mi. SE of monument entrance, 4000 ft. elev., 1♂, 3 August 1989. Covington Flats, 0.4 mi. N of Monument boundary, 4220 ft. elev., 1♂, 10 August 1989. Kelso-Cima Rd., 6.3–11.5 mi. N of Kelso, 2820–3480 ft. elev., 2♂, 1 November 1992. Hwy 247, 10 mi. S of I-15 at Barstow, 2840 ft. elev., 1♂, 7 November 1992. **Kramer Jct., 3.1 mi. E on Hwy 58, 2470 ft. elev., 1♂, 8 November 1992. San Bernardino and Kern Co. lines (Red Mtn. area):** 19–23 mi. N of Kramer Jct. on Hwy 395, 0.5–1.5 mi. W of highway, 3220–3400 ft. elev., 2♂, 20 October 1989; 3200–3280 ft. elev., 4♀, 12–14 October 1991; 3♂, 26 October 1991; 1♂1♀, 13 October 1992; 1♀, 22 January 1994. **Kern County:** California City, 7.6 mi. E on

Table 13.—*Aphonopelma angusi*, allotype female (= *A. iodium*): leg and pedipalp segment lengths.

	I	II	III	IV	Palp
Femur	7.35	6.70	6.15	7.55	5.40
Patella	4.00	3.65	3.30	3.60	3.10
Tibia	5.55	4.70	4.15	5.90	4.00
Metatarsus	4.85	4.70	5.20	7.30	
Tarsus	4.00	3.80	3.90	4.50	4.10
Total length	25.75	23.55	22.70	28.85	16.60

Table 14.—*Aphonopelma idium*, females (14): range of leg and pedipalp segment lengths.

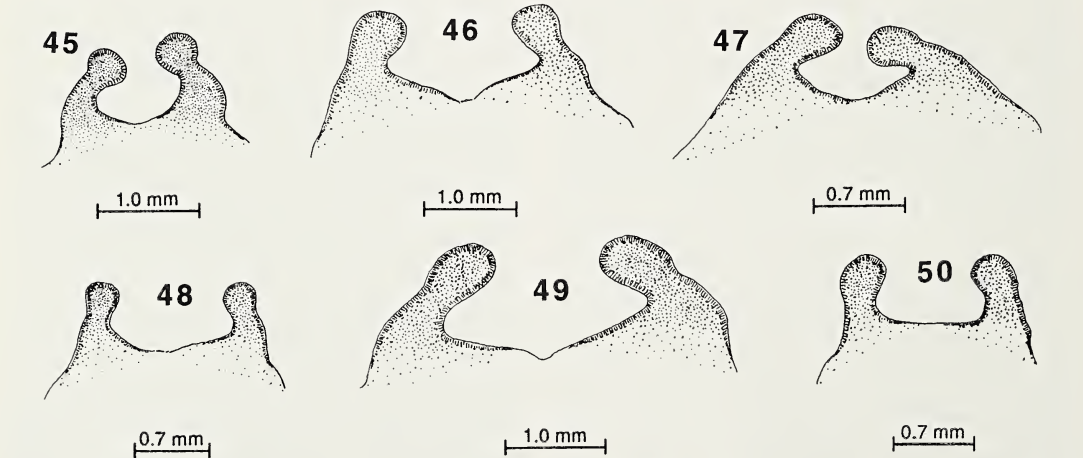
	I	II	III	IV	Palp
Femur	9.10–17.00	8.40–15.85	7.90–14.60	9.65–17.30	6.90–12.50
Patella	4.95–9.10	4.55–8.60	4.15–7.85	4.55–8.30	3.65–6.80
Tibia	6.80–12.40	5.90–11.20	5.35–10.00	7.30–12.40	4.90–9.00
Metatarsus	6.20–13.30	6.00–12.80	6.65–13.70	9.05–17.95	
Tarsus	4.70–8.80	4.50–8.60	4.70–8.60	5.10–9.30	5.00–9.00

Twenty Mule Team Rd., 2710 ft. elev., 1♂, 20 October 1991. *Inyo County*: Deep Springs Valley, approx. 2 mi. E of Westgard Pass on Hwy 168, approx. 5000 ft. elev., 1♂, 16 October 1976 (Frank Hovore); Big Pine, 2.3 mi. E on Hwy 168, 4320 ft. elev., 1♂, 20 October 1993. **NEVADA**: *Clark County*: Pahrump, 17–19 mi. SE on Hwy 160, 3400 ft. elev., 1♂, 11 October 1974 (W. Icenogle). Searchlight, 3 mi. S on Hwy 95, 3250 ft. elev., 1♂, 2 October 1981 (W. Icenogle). 8.2 mi. W on Hwy 164, 2 mi. N to foothills of Highland Range, 4330 ft. elev., 1♂2♀, 7 October 1989. **UTAH-ARIZONA**: *Washington County, UTAH and Mohave County, ARIZONA*: Male specimens collected between 2320–4330 ft. elev. in Castle Cliffs, Summit Springs, and Welcome Springs areas on southern slope of Beaver Dam Mountains and close to Utah-Arizona border on both sides of state line off old Hwy 91, 1imm♂, 4 July 1989; definitive molt, 8 September 1989; 1♂, 16 September 1989; 1♂, 23 September 1989; 3♂, 6 October 1993; 1♂, 12 October 1993; 5♂, 19 October 1993; 1♂, 20 October 1993. Female specimen collected in Summit Springs area in Beaver Dam Mountains, 3650 ft. elev., 1♀, 5 October 1993. All specimens collected

by the author unless otherwise indicated. Specimens collected by the author deposited in AMNH.

NATURAL HISTORY

**Habitat.**—*A. joshua* new species and *A. mojave* new species, only narrowly sympatric (near Yucca Valley, California), appear to have similar ecological requirements throughout their ranges. Both burrow in soil of like composition, inhabit comparable vegetation communities, and occur at elevations between 550–1600 m. *A. mojave* has been found at slightly lower elevations near Trona, California, and *A. joshua* also inhabits biomes characteristic of the Sonoran Desert (southeastern JTNM). Both species prefer flat or gently sloping terrain composed of sandy soil of various particle size. *A. idium*, sympatric with both *A. joshua* and *A. mojave* throughout their respective ranges, occurs at elevations below 300 m in the basins and above 1700 m on the



Figures 45–50.—Spermathecae of *Aphonopelma idium*. 45, *A. angusi* allotype (= *A. idium*); 46, Searchlight, Nevada; 47, 48, Red Mountain, California; 49, Quail Mountain, JTNM; 50, Pleasant Valley, JTNM.



inter-desert and perimeter mountain slopes and is equally common on steeper and/or rockier hillslopes and in regions where the substrate is rich in clay content. Because of the increased tolerances of *A. iodum* to varied substrate consistencies, xeric conditions, and cooler, mildly hydric climates, it has succeeded in accessing regions that are unsuitable for *A. mojave*, both within the Mojave and to the north, in the Great Basin Desert. The xeric drainages that divide *A. mojave* into eastern and western races, the rocky, rugged terrain between Las Vegas and the Mormon Mountains that apparently isolates northeastern *A. mojave* populations, and the mountainous regions to the north of St. George were not found to be geographic barriers for *A. iodum* (a corridor, 1700 m in elevation, snakes through Utah from the BDM to the Idaho border (Salt Lake City to Provo to Nephi, west to Jericho, south to Delta, to Black Rock, to Milford, to Lund, east to Cedar City, and finally south to St. George between the Pine Valley Mountains and the Hurricane Cliffs); two specimens from Utah and one from California were found at elevations greater than 1670 m).

All Mojave species are common in vegetation communities dominated by Creosote Bush (*Larrea*), often in pure stands or in association with either bursage (*Ambrosia*), brittlebush (*Encelia*), or Joshua-tree (*Yucca*), and by Joshua-tree and perennial bunchgrass in association with Creosote Bush and/or sparsely distributed blackbrush (*Coleogyne*). Communities within which *A. iodum* is relatively common (but not usually abundant) but *A. joshua* and *A. mojave* rare or absent, are dominated by saltbrush or bursage at low elevations (below 600 m) and by Blackbrush, Big Sagebrush (*Artemesia*), and juniper or mixed juniper and pinon at high elevations (above 1500 m).

**Daily activity patterns.**—After initially unplugging their burrows following the cool winter months, the Mojave *Aphonopelma* deposit silk around entrance perimeters to a greater or lesser extent; and over time many layers of silk accumulate. During daylight hours of the ensuing months most burrows have a sheet-like layer of silk (common in all three species) or a loose plug of silk-bound earth (less common and only in *A. joshua* and *A. mojave*) blocking the entrance (obstruction

of the entrance may ward off certain potential day-time predators such as ants and help maintain higher humidity in the burrow). Usually after dark or, less frequently, just before sunset when overcast or cloudy, females and immatures were commonly seen just inside their burrows or a few centimeters below the entrance. Only after dark (all observations) were the silken coverings and plug removed, the silken sheets torn down and flattened against the perimeter and inside wall of the burrow, the plugs either pushed with forelegs or carried in the chelicerae (with the aid of the palps) to the outside of the burrow. After removal of these obstructions the majority of spiders, initially, remained motionless within the burrow confines, completely submerged in the upper level or with forelegs resting over the perimeter. After varying intervals of time many individuals then exited their burrows, eventually to assume a waiting position. Deposition of additional silk around the entrance perimeter was one of the first activities of the resident, once above ground, followed by (rarely preceded by) intermittent, brief periods of wandering, between which the waiting posture was assumed. *A. joshua* and *A. mojave* rarely ventured more than several cm from the entrance (except when in pursuit of prey) although individuals of both species were observed at distances of up to 30 cm. The larger *A. iodum* were commonly observed at distances of 30 cm or less and, rarely, of up to one meter.

**Seasonal activity.**—Seasonal activity is defined by the period of time between which burrows of a given species are first unplugged after winter and then replugged for the following winter. The presence of fresh silk around the entrance perimeter, recently excavated material around the burrow, or a thin sheet of silk covering the burrow's entrance were indicative of desert *Aphonopelma* activity. Conversely, an open burrow lacking silk around the entrance, accumulated dust on the perimeter silk, or a burrow with a hardened plug or turret were indicative of inactivity.

Active burrows of *A. joshua* were found between the end of March and the last week of October, those of *A. mojave* between the first week of April and the first week of January, and those of *A. iodum* throughout the year. In *A. joshua* the vast majority of burrows were plugged by early October but in *A. mojave* not





Figure 51.—Burrow of *Aphonopelma joshua* new species (female) showing typical turret made by the species; the shadow cast by the turret gives an indication of its height (*A. mojave* new species turrets are indistinguishable from those of *A. joshua* new species).

until middle or late November. Activity within *A. joshua* was abundant by mid-spring and through the species summer breeding season but steadily declined thereafter. In contrast, activity within *A. mojave* was minimal until close to the beginning of the species fall breeding season, peaking by mid-October; winter plugging coincided with the termination of the breeding season. *A. iodium* was commonly found between early March and mid-December, but activity was most abundant in late summer and during the species fall breeding season. Open burrows were infrequently discovered in January and February, and then, only in the central and southern portions of the species range.

Usually prior to or during respective breeding seasons, excavations composed of silk-bound soil, sclerotized remnants of prey, and old exuviae were deposited outside of the burrows in a species dependent fashion; only a few individuals excavated (any material) in spring. Both *A. joshua* and *A. mojave* formed indistinguishable turrets (Fig. 51) with the excavations that surrounded and elevated the entrance (the vast majority of turrets formed within a given year were washed away by the hard winter rains leaving no trace of the burrow's location; the few that were not destroyed had become hardened mounds that were built upon with new excavations prior to or during the subsequent breeding season).

Turrets as high as 13 cm were found although most were less than 6.5 cm, with the average outside diameters approximately 5–6 cm. The inside turret walls were usually lined with silk which continued over the entrance and partially or completely blanketed the top of the mound. *A. iodium*, on the other hand, scattered excavations loosely around (rarely, appearing slightly mounded) or to one side of the burrow, often at some distance from the entrance; excavations were infrequently found by burrows known to contain medium to large size females. Entrance perimeters were generally lined with copious layers of silk which extended up to several centimeter both over the substrate and into the burrow; the entrance almost always opened at substrate level. Excavation by all species, although often intermittent, generally appeared to be a continuous process throughout respective breeding seasons. A proportion of each species replugged their burrows on a routine (observed only during a breeding season), irregular (for relatively short durations), or extended period (observed for up to two months) basis during their seasonally active months. Minch (1979) reported both intermittent and extending plugging by *A. chalcodes* Chamberlin. In the Red Mountain area several *A. mojave* burrows were regularly plugged (from one to three days observed) and reopened (only one night observed) during the fall breeding season; plugs were usually in place well before sunrise and pushed aside only after dark. Other burrows, previously not plugged but covered by a sheet of silk during the day, were plugged in late September and early October, reopened in late October toward the end of the breeding season, and shortly thereafter, replugged for the winter. One burrow, found plugged at the beginning of the breeding season, appeared to have been recently active because of its only slightly hardened turret (turrets that were plugged or otherwise inactive for long periods of time developed a windblown, smoothed appearance and very hardened outside walls; new silk and excavation were lacking); and its occupant removed the plug and began to excavate in the last week of October. Summer plugging (Minch 1979) by *A. mojave* was observed only in captives, several of which plugged their burrows prior to a subsequent summer molt, one prior to producing an egg sac; several others simply sealed the entrance



with silk before molting. Since gravid females and females with egg sacs were rarely found during the summer months (and then, in burrows with only silken sheets covering the entrance), I suspect that most do not become seasonally active until their young are ready to disperse. Summer plugging by *A. iodium* was not uncommon but burrows were rarely found plugged during the species breeding season. One burrow (in JTNM) plugged before 5 August was reopened between late September and 12 October and remained open for the duration of the breeding season.

Minch (1979) reported that the maximum duration of winter plugging by *A. chalcodes* (female) was between 644–674 consecutive days. One immature and two female *A. paloma* were taken from inactive burrows (burrows were not detectable other than by my markings and had been monitored monthly) on 19 November 1992 (near Sentinel, Arizona), at least 711 days after they were plugged prior to 9 December 1990. Although these data are lacking for the Mojave *Aphonopelma*, burrows (and wandering males) of all species were abundant throughout the Mojave in 1989 but were difficult to locate in 1990. Again in 1991 burrows were abundant, found in even greater numbers than in 1989. Yearly burrow density fluctuations at all study sites (for each species) followed this larger scale trend. Such observations lead me to believe that extended plugging within desert species may be similar in duration to that observed in *A. chalcodes* and *A. paloma*.

**Burrow construction and remodeling.**—Although all observed *Aphonopelma* species can construct their own burrows, evidence indicates that most individuals that have abandoned or been displaced from their burrows will adapt any suitable cavity. In captive situations intentional burrow damage by the investigator initiated new burrow construction by the former occupant only if no other cavities were available. In similar field experiments, a ‘homeless’ spider sought shelter in the first sufficiently large unoccupied burrow or subterranean cavity encountered. Recent occupancy was suggested when a burrow was found with unplugged side tunnels or was significantly wider in diameter than usual for the size of the resident. Whether growing tarantula spiderlings (under natural conditions) continue to enlarge and remodel initial bur-

rows or seek larger burrows as needed is not known although all *Aphonopelma* I have had in captivity continued to utilize initial burrows through their frequent enlargement.

Most desert captives eventually plugged pre-existing burrows only to resurface either back through the plugs or through new shafts. Entrance and upper burrow diameters were consequentially reduced and in the majority of burrows were correlated with occupant size. Natural entrance diameters for *A. iodium* ranged from approximately 1.2–2 times greater than the width of the carapace and those for *A. joshua* and *A. mojave* from 1.5–2 times greater. Minimal diameters may prevent intrusion by slightly larger, more powerful predators or conspecifics, lessen the effects of erosion, especially when burrows are reopened through a plug, and help to maintain optimal humidity within the burrow.

Burrows of *A. joshua* and *A. mojave* extended more or less vertically to depths between 25–53 cm. Well established burrows (those with side chambers packed with discarded food remains and pieces of old exuviae) were usually the deepest. Throughout most of their length typical burrows were larger in diameter than at subsurface and entrance levels although were commonly constricted in up to several regions, one of which was usually near or adjacent to the horizontally inclined terminal chamber. Side tunnels and shafts beyond certain depths were usually plugged with silk-bound earth and shallow burrows were presumed to have been excavated to appropriate depths based on the varying quantities of excavated material found outside the entrances (other than during breeding seasons). The average depth of *A. iodium* burrows was approximately 45 cm, ranging from 30 cm to 1 m. Their tortuous burrows commonly ended in horizontal chambers similar to those of *A. joshua* and *A. mojave*. Short side chambers in well established burrows were generally located near the bottom and were used as dumpsites for accumulating food debris, old exuviae, and discarded egg sacs.

**Molting cycles.**—Molting cycles are known primarily from captive specimens (observation over several years for most juveniles). Immature and adult female *A. mojave* (16 adult) generally molted between mid-July and mid-August. However, one immature female molted as early 22 May and two females

molted after 11 August, one immature and one adult on 7 and 9 September, respectively. Definitive molts of three males occurred between late August and the first week of October. Immature male cycles were coordinated with female cycles. In *A. joshua*, penultimate males collected within 7–8 months of maturity molted between 7 July–1 August (just prior to or during their breeding season). Subadult males collected within two or three molts of maturity molted as early as 24 June and as late as 1 September. Juveniles (except those molting more than once a year) and females molted between 8 June–7 August. In *A. iodinium* juveniles and females were known to molt between late May and early October, the majority molting in July. One immature female was found in its natural burrow 23 September 1989 (BDM) with not yet fully sclerotized fangs, indicating a very recent molt. Two captive males (penultimate instars when collected), one from the BDM (Utah) and one from the Mid Hills area (east Mojave), molted 8 September and 2 August, respectively.

Both Minch (1979) and Baerg (1958) found molting to be predominantly an annual event except in rapidly growing spiderlings and young juveniles (Baerg and Minch), in females producing eggs (Minch), and in older females (Baerg). However, a proportion of juveniles and subadults and an even larger proportion of adult females in captive Mojave *Aphonopelma* failed to molt annually. Under natural conditions it was not uncommon to find unusually faded specimens, a condition indicative of a skipped molt. Old females (age estimated by relative size) were infrequently found not only with pubescence very bleached but worn away in various areas on the legs, carapace, and chelicerae. Such females may have weathered two or more consecutive years without molting. Baerg observed that Arkansas females (*A. hentzi*) producing egg sacs delayed molting until shortly after dispersal of the young. Minch noted that female *A. chalcodes* producing egg sacs failed to molt in that same year. In agreement with Minch, I observed that captive females (*A. joshua* and *A. mojave*) subsequently failed to molt in the year they produced egg sacs but molted the following year. Similarly, females (*A. joshua*-1, *A. mojave*-3, *A. iodinium*-1) taken from the field with egg sacs failed to molt until the following year. When burrows were unearthed

during or shortly after a breeding season, recently discarded egg sacs were not found with females appearing to have molted within the year; coloration of females was faded when such egg sacs were found, indicating skipped molts. Apparently most Mojave Desert females are not able to acquire the nutritional reserves necessary for egg production and subsequent molting activity.

**Sperm webs.**—Sperm webs of the desert species are typical of those described by Baerg (1958) of *A. hentzi*. In using his detailed accounts of male behavior during web construction as a comparative reference I found no distinguishable differences between corresponding behaviors of *A. hentzi* and the Mojave species (captive males).

Initial webs of *A. joshua* males were constructed inside the burrow, if sufficiently wide in any region or, otherwise, outside the burrow between three and twelve days after definitive molts (this agrees with Baerg's field observations). Most natural burrows, however, did not appear to have the necessary space for such activity. Baerg observed individual males constructing as many as 17 sperm webs in the course of six weeks and others as few as one in their mature life. From eight males I reared to maturity the number of webs constructed per individual varied from one to four. One male produced two webs within four days while a second produced four webs within 19 days, both without exposure to females. Several field collected males produced one or more webs in captivity while others failed to spin a single web. One male collected 28 July 1992 spun two webs without exposure to a female, one shortly after confinement and a second almost a year later in June 1993 (this specimen, incidentally, seemed to be an exception to the general rule of longevity among males of most *Aphonopelma* species; even captive males rarely last through the year in which they matured).

Initial sperm webs of three captive-reared *A. mojave* males were produced within 10–21 days after definitive molts; only one produced a second web (date unknown). One field-collected male produced a maximum of three webs, each spun within two days after successive matings; a second male produced two webs without introduction of a female while a third male produced one web two days after mating but failed to produce another web after



mating with second female. Other males spinning only one web were never exposed to females in the laboratory.

**Seasonal mating activity.**—Within temperate region *Aphonopelma* there are two basically distinct breeding seasons: one commencing in summer and the other in fall. Males of the summer breeding species generally search for females between mid-July and early September. Males of most fall breeding species are first seen in middle or late September but are infrequently found after mid-November. However, in two fall breeding species (*A. paloma* and an undescribed species from SE Arizona) the onset of male activity is delayed until late October or early November; most activity has ceased in these species by late November and by mid-December (late December in undescribed species) males are rarely seen. I have noticed that within most California and Arizona *Aphonopelma*, irrespective of breeding season, stragglers are occasionally found long after other conspecifics have perished. Early males (Baerg 1958), on the other hand, seem to occur only in the fall breeding species but are found in significantly reduced numbers from those occurring during the fall months. Two of the three Mojave species, *A. iodium* and *A. mojave*, are fall breeders; early males are known to occur only in *A. iodium*. The third species, *A. joshua*, is strictly a summer breeder.

*A. mojave* males were seen searching for females from early October until nearly the end of November. The earliest collection record for a male is 5 October (1973, W. Icenogle) and the latest, 24 November (1991). All observed mating activity was diurnal. Males were found between 0800 h and late afternoon shortly before sunset; a single male was collected after sunset on a warm, humid evening (25 °C). On cooler days (when early morning and late afternoon temperatures were below 15 °C) males became active later in the morning and took shelter earlier in the evening.

*A. iodium* males (fall males only) were collected between 16 September (BDM) and 29 November (southern Nevada, by W. Icenogle). Breeding activity in this species is believed to be primarily diurnal although some nocturnal mating may also occur; the majority of males were collected between 0900–1600 h, a few as late as 2230 h on warm evenings (over 20

°C). Summer males, believed to be nocturnal breeders, were collected in August (of three different years in JTNM) and only after dark between 2200–0100 h. Baerg believed that early males were survivors from the previous year that had somehow managed to overwinter and that their success in mating at this time was doubtful. All summer males collected in JTNM were in excellent condition and appeared to have molted quite recently. Since Baerg observed that mature female and immature Arkansas tarantulas begin their molting cycles toward the end of July and I have recorded molting periods of captive *A. iodium* from mid-June to mid-September, it seems quite possible that these summer males had not overwintered but had, instead, recently matured. Since many females have molted and become active by August it seems likely that early males are successful in their breeding attempts. Observations of two captive males (molting 2 August and 8 September, respectively) suggest that differences in temporal spacing between maturing molts and burrow abandonment and in the timing of the molt itself, in combination, may account for both the presence of summer males and the duration of the primary breeding interval. Following its September molt the latter male remained in its burrow for six weeks, emerging only for relatively short periods of time to eat, drink, and, eventually, construct its first sperm web. Its behavior in conjunction with its maturation date may be typical of circumstances leading to the emergence of the more prevalent fall males. On the other hand, the former male became very active within two weeks of its early August molt, rarely returning to its burrow. Its early maturation and hastened restless behavior may be indicative of events leading to the presence of the much less common summer males. In captive males prolonged lingering between definitive molts and burrow abandonment is the more commonly observed behavior.

*A. joshua* is the only Mojave Desert species known to be strictly a summer breeder. Of the males that I have collected the earliest was taken 20 July (1989), the latest 6 September (1992). However, E.L. Sleeper and S.L. Jenkins collected one male 9 September (1966) and a second 23 September (1967), both from pit-traps in JTNM. All observed mating activity was nocturnal. Males were collected be-

tween 2100–0245 h (only two after 0100 h) and were generally seen in greater numbers on warm, humid evenings.

**Mating behavior.**—Most mating behaviors such as male courtship, female response, and post contact performance were correspondingly indistinguishable between the desert species and from the respective behaviors of *A. paloma* (Prentice 1992). Duration of copulatory contact under natural conditions varied within all species although the respective ranges were very similar; the maximum time value of sustained contact for each species was observed under laboratory conditions. Male exploration of contacted burrows varied slightly with the entrance type; males generally located non-turreted burrow entrances more quickly than those atop turrets. Males stridulated periodically during frequent pauses in their search for female burrows.

In their initial inspection of female burrows typical *A. mojave* males slowly circled the outer turret wall, systematically pausing with palps in direct substrate contact as if chemically assessing female receptivity. Whether turrets function as pheromone beacons is not known although males sometimes left turreted burrow after brief investigation without initiating courtship. Males continuing their inspections usually proceeded toward the top of the turrets, frequently arresting their forward progress to alternately stridulate (characterized by bobbing up and down) and forcefully tap the turret walls with both front legs and palps simultaneously. Tapping and stridulation were executed with more regularity once female entrances were located, with one to several spaced taps alternating between stridulatory pulses. If there was no immediate female response, males frequently extended their forelegs into the turret or crawled partially or completely inside while continuing to tap and to stridulate if the hind two pairs of legs were free of the entrance. At various stages of courtship, receptive females generally emerged. A drumming response (Prentice 1992) by the female before emergence was observed in several instances when females could be seen in their burrows and in captive situations after male courtship had been initiated. Female drumming (with both pairs of forelegs) was always observed to follow male stridulation but not leg tapping. Once contact between a pair was made, the female com-

monly rushed the male pushing him backwards a few centimeters until he secured her fangs. In one instance, a Red Mountain female, courted by a male having his front legs inside the burrow, exploded from the entrance backing the male almost instantaneously to a distance of 20 cm; after much leg grappling the male finally managed to secure the female's fangs. Copulatory contact in several field matings was sustained for slightly less than one minute to just under three minutes.

In pairings of *A. joshua* differences in laboratory (when females were in burrows) and field behavior could not be detected except in duration of copulatory contact. Contact between several laboratory pairs was sustained for 1–10 minutes. For field observation males were released at night by female burrows under artificial, dim light conditions which made accurate observation difficult. Contact under these conditions was sustained for 1–1½ minutes in two pairings. In all observations uncoupling proceeded with the male releasing one of the female's fangs while simultaneously pulling away to position himself for rapid departure (true of all Mojave *Aphonopelma*). All other associated behaviors appeared to be identical to those of *A. mojave* when the courted female was in a turreted burrow. Male stridulation was audible in the laboratory when background noises were at a minimum and was nearly comparable in amplitude to that generated by the much larger *A. reversum* Chamberlin; I have not heard male stridulation in the field.

Under natural conditions, *A. iodium* males usually initiated courtship more rapidly after detecting female silk than males of either *A. joshua* or *A. mojave*. At times, females emerged during the initial stages of courtship before the male had physically located the burrow entrance, generally a rapid process for these males. Duration of copulatory contact was maintained for as little as 30 sec and for as long as 3 min; under laboratory conditions contact was sustained for up to 6 min. Females pursued males after uncoupling much more often than did females of either *A. joshua* or *A. mojave* although pursuit, in general, was relatively rare. In no field observation (all species) was a male caught by a female; under laboratory conditions, males with limited running space were occasionally caught and killed by females.



**Egg sacs, fecundity, and spiderlings.**—

Data for *A. joshua* were gathered from two females producing egg sacs in the laboratory and from one female guarding an egg sac when collected. One female (carapace length, 6.5), collected 19 April (1989), excavated and promptly plugged a new burrow in mid-May. A cocoon was produced in the burrow between 23–25 June which, when finished, was a wrinkled, spherical mass approximately 12 mm in diameter. By 26 July the egg sac was very swollen and smooth, suggesting that the eggs had hatched. Between the end of July and 12 August darkened forms appeared inside of the cocoon; third instar (fourth post-embryonic stage; third stage free of chorion; first mobile stage – Galiano, 1969, 1973) develop most leg spines and urticating hair patches beneath the semi-transparent integument, molting to fourth instar within the egg sac (pers. obs.; also consult Galiano 1973). On 19 August the first of the young appeared on the outside of the egg case beside a small exit hole. On 21 August approximately 40 young were counted, a few of which were observed outside of the burrow less than 1 cm from the entrance. By 25 August approximately half of the spiderlings were roaming about in the terrarium, periodically returning to the burrow to take refuge. More than three-quarters of the young had permanently dispersed by 30 August. A total of 51 young was counted, all of which had successfully escaped the egg sac. A second female (allotype), collected 21 October (1989) from a plugged burrow, produced an egg sac between 22–27 April (1990) in the burrow she had excavated shortly after confinement; she consumed the eggs two weeks later. Neither of the preceding females was observed without at least one of its fore-appendages in contact with the egg sac (also Minch 1979). A third female (carapace length, 7.60, following its 1993 molt) was guarding an egg sac when excavated from its burrow 30 July (1992). There was a small emergence hole in the cocoon but only two spiderlings were observed on the visible surface. Forty-one 4th instar, three 3rd instar spiderlings that failed to molt successfully, and four desiccated eggs were counted when the cocoon was opened. Due to the breached condition of the egg sac, the actual number of viable young may have been higher. Fourth instar spiderlings of the female that produced a cocoon in the labora-

tory began to appear outside the egg sac approximately seven weeks after eggs were deposited. If it may be assumed in this case that field conditions roughly paralleled laboratory conditions, the female producing a cocoon in the wild would have deposited her eggs during early June, seven weeks prior to the appearance of the first young. Baerg (1958) observed that females of *Dugesiella hentzi* deposited eggs in late June or early July with an incubation time of 45 and 65 days under laboratory conditions; Gertsch (1979) roughly estimated an incubation time of 6–7 weeks for 'local' tarantulas in general.

Dissection of an *A. mojave* female (carapace length, approximately 8.5) revealed a complement of 186 developed eggs and 150–200 small developing eggs. Three females produced egg sacs in the laboratory but cannibalized them before they could be removed; all were produced between the last week in June and the second week of July. Of three females that were excavated from their burrows 7 October (1989) near Searchlight, Nevada, two were accompanied by what appeared to be fourth instar young, one with 18 (not preserved), the second with 15 (carapace lengths, 1.7–1.8). The third female had a complement of 20 young, 5 with carapace lengths of 2.5–2.8, 14 with lengths of 3.0–3.3, and one with a carapace length of 4.1. Data from laboratory reared spiderlings suggest that the young of this female were at least second year spiderlings, or third year in case of the largest young, that were still tolerated or even guarded by the female. Carapace lengths of reared spiderlings of three species did not reach 2.5 until the second year for the two larger species, *A. behlei* and *A. iodium*, and until the third year for *A. joshua* (closely approximating *A. mojave* in size).

Only fecundity data were obtained for *A. iodium*. The larger of two females (carapace length, 15.8), collected 7 October (1989) near Searchlight, Nevada, was dissected and contained an estimated 800–1000 developed and developing eggs. The smaller female (carapace length, 11.5) was collected while guarding her brood, many of which were on or near the cocoon. My initial estimation of spiderling numbers was approximately twice that of the 65 eventually retrieved; a substantial portion may have escaped into subterranean crevices when the cocoon was removed. Another factor



that may have lowered the natural count was the possible dispersal of young before the burrow was disturbed. Nevertheless, data suggest that larger females are capable of producing more offspring.

**Prey capture and prey.**—Tarantulas, as in other poor sighted hunting/ambushing spiders, detect their prey through substrate vibrations generated by movement. Capture methods of all Mojave *Aphonopelma* were, typically, indistinguishable. Once vibratory information was received, *Aphonopelma* usually turned toward the direction of the source. If the prey was relatively near and produced vibrations of the appropriate magnitude, it was quickly rushed, scooped toward the spider's unfolding fangs with fore-legs (or with larger prey with all legs), and impaled almost simultaneously. Once the quarry was secured, *Aphonopelma* typically extended their legs, raising the sometimes struggling victim well above the substrate, thus minimizing its chances of escape by using the ground surface for leverage. Most spiders then immediately returned to their burrows, inside of which the meals were consumed. If vibratory stimuli were further away, *Aphonopelma* moved toward the source through a series of discreet advances, reassessing direction, proximity, and magnitude of the vibration with each movement of the prey; the attack sequence was the same once initiated. Prey was pursued by *A. joshua* and *A. mojave* for distances up to 20 cm (rarely, up to 30 cm) and by *A. idium* for up to 50 cm (rarely, up to greater distances) from the burrow entrance. Both *A. mojave* and *A. idium* were lured out of their burrows (by using a twig or blade of grass to imitate prey movement) when nighttime temperatures were as low as 7 °C (2 °C in *A. paloma*), suggesting that threshold temperatures for feeding are lower than those required for initiation of male wandering and courtship behavior.

Sclerotized remains of beetles (primarily in the family Tenebrionidae), small-to-medium size scorpions, spiders of other families, and orthopterans were found in both burrow chambers and excavations of *A. idium*; beetles comprised the bulk of the recognizable remains. Prey of both *A. joshua* and *A. mojave* included various species of beetles (primarily tenebrionids), harvester ants (Myrmicinae), small orthopterans, and, occasionally, small scorpions. Soft bodied insects, centipedes, and

small lizards were consumed by captive *Aphonopelma*. Evidence of neither congeneric nor conspecific cannibalism was detected among any of the sclerotized food remnants examined although S. Kutcher (16 October 1990) collected a male *A. idium* clutching a male *A. mojave* in its fangs during the species common breeding season. In the laboratory, captive spiderlings past dispersal age occasionally cannibalized each other under overcrowded conditions; males with insufficient space to escape were sometimes killed by females after mating and, presumably, would have been consumed if not removed.

**Isolating mechanisms in sympatric species.**—A widely accepted paradigm is that, for the maintenance of closely related species in sympatry, some form of isolating mechanism must be in place. Because of their adaptive value premating mechanisms are believed to be of greater evolutionary significance than postmating mechanisms. Since the morphologies of both the male palpal bulb and the female spermathecae in *Aphonopelma* species (those in which male embolus is slender), doubtfully, preclude copulatory success, significant size differences in concurrently breeding species would reduce the likelihood of interbreeding attempts both because of physical constraints and differences in the magnitude of vibrational stimuli produced, the latter possibly eliciting a feeding response in the larger species and a flight response in the smaller species. Males may distinguish conspecific female burrows by entrance diameter although chemical cues, undoubtedly, play a more important role in species recognition. One possible mechanism among species of subequal size is a behavioral skew in breeding seasons; with this energy conservative mechanism in place, such species could coexist with minimal contact.

Field observations suggested the presence of such mechanisms among temperate North American sympatric *Aphonopelma*. Species of similar size had distinct, non-coinciding breeding seasons as well as morphological dissimilarities in metatarsal scopulation and/or coloration or in condition of tarsus IV scopula (entire or partially divided). Concurrently breeding species were found to be significantly different in size and generally distinctive in carapace and leg (in females) coloration and in degree of metatarsal scopulation.



The following examples illustrate the breeding season/size related mechanisms and associated morphological differences in known sympatric species (no species other than those referred to have been found in the stated areas of sympatry): (1) *A. joshua* and western *A. mojave* are narrowly sympatric and completely overlap in size (also sympatric with *A. iodum*); the former is a summer breeder, the latter a fall breeder; partial division of tarsus IV scopula, limited distribution of red-orange dorsoabdominal setae, and swollen third femur of males are the obvious character differences that distinguish *A. joshua*. (2) *A. iodum* and *A. mojave* are both fall breeders (also sympatric with *A. joshua* near Yucca Valley); the former are usually much larger than the latter (the smallest *A. iodum* have been found in southern Utah but are substantially larger than the largest *A. mojave* in that region); extent of metatarsal scopulation and carapace coloration are obvious dissimilarities. (3) Two species, very similar in size, inhabit the coastal and inland regions south of the southern California transverse mountain ranges; one is a fall breeding 'eutylenum type' (preliminary data suggest that Chamberlin names for 'eutylenum type' species described from these areas are synonyms), with typical coloration and extensive metatarsal scopulation; the other is a summer breeder (*A. reversum* Chamberlin) is solid black (unless faded but is still unicolorous), and has limited metatarsus III and IV scopulation. (4) In Arizona *A. chalcodes* Chamberlin and *A. behlei* Chamberlin are narrowly sympatric in several regions at elevations approaching 1800 m (females overlap in size while *A. chalcodes* males are larger); *A. behlei* (mountain top or high elevation species) is solid black in color, has limited metatarsus IV scopula, and breeds in fall while *A. chalcodes* (primarily a desert dweller) has accentuated 'eutylenum type' coloration, more extensive metatarsus IV scopula, and breeds in summer.

The following examples illustrate the responses of Mojave Desert tarantula pairs in situations where both supposed conspecific and interspecific pairings were made: (1) In laboratory breeding experiments two *A. joshua* males were introduced to *A. mojave* females, and two males of the latter species were paired with females of the former species. Pairings were made in both August and

October to even out seasonal bias. Males of both species began courtship displays and females responded by typical drumming in three instances, two of which were by *A. joshua* females. In all four pairings both genders quickly withdrew when contact was made by moving rapidly in opposite directions. That post-contact mating attempts were never initiated suggests that each species may have unique contact pheromones that function in species recognition and as a secondary isolating mechanism in areas of sympatry. (2) Eastern and western *A. mojave* males readily courted females of the differing race both in the laboratory and under natural conditions. Once females indicated receptivity, copulatory contact was made and sustained in all pairings for varying periods of time. (3) In similar experiments with 'eutylenum types' from various regions of the Mojave Desert courtship and response behaviors were succeeded by sustained contact during which copulation occurred; the following males and females were paired: two male from the Beaver Dam Mountains with females from Red Mountain (west Mojave) and the Providence Mountains (east Mojave), respectively (the latter pairing was in mid-October at the female's natural burrow); a male from Searchlight, Nevada with a Red Mountain female; a male from Joshua Tree National Monument with a female from Lucerne Valley, California. When paired with *A. mojave*, female *A. iodum* exhibited only predatory behavior; similar behavior was seen in male *A. iodum* although they infrequently ignored females; *A. mojave* exhibited only a flight response.

Expected responses to interspecific pairings between sympatric 'eutylenum type' species and between species similar to *A. mojave* would be on the order of those seen in pairings of *A. joshua* with *A. mojave*. Instead, the above pairs freely mated, supporting both the synonymy of *A. iodum* and the conspecificity of eastern and western *A. mojave*.

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## ***CALLOBIUS GUACHAMA* (ARANEAE, AMAUROBIIDAE): HABITAT, DISTRIBUTION AND DESCRIPTION OF THE FEMALE**

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**ABSTRACT.** On the basis of one male specimen, *Callobius guachama* Leech 1972 was first established during the familial revision of the Amaurobiidae. We have collected additional specimens of this spider and, herein, provide a description of the female as well as notes regarding the habitat and distribution of this large, montane spider.

In the familial revision of the Amaurobiidae (Leech 1972), *Callobius guachama* was named on the basis of a single mature male spider collected inside a domicile near the foothills of the San Bernardino mountains. We have recently collected additional specimens in natural environments or have had specimens sent to the University of California Riverside Department of Entomology for identification. In addition to providing habitat and collection information for the species, we describe the female of *Callobius guachama* for the first time.

Leech (1972) states that the internal genitalia for all amaurobiid genera except *Titanoeca* Thorell 1870 are not useful for taxonomic differentiation at the species level. Therefore, in remaining consistent with the familial revision, we configure here the ventral and posterior views of the *C. guachama* epigynum. Also, only the diagnostic characteristics of the male palp (i.e., tibia, median apophysis) were illustrated in the familial revision. As a record of completeness for this species, we include conventional ventral and lateral views of the entire male palp of *C. guachama*.

### **METHODS**

All preserved specimens were examined under alcohol and measured with a Wild 5A microscope fitted with an ocular micrometer; all measurements are in millimeters. If the abdomen of an alcohol specimen did not appear shriveled or was not damaged in the collection process, body length measurements were taken. Several spiders were collected as im-

matures, as reflected in the collection data, but were maintained in the laboratory and examined as preserved mature specimens. Physical description of the female is presented from live specimens as well as preserved material. The physical characteristics for the males examined here follow that of Leech (1972) for the holotype. The acronyms used in this paper are as follows: AMNH–American Museum of Natural History, N. Platnick; BRH–B.R. Hébert (pers. collection); CAS–California Academy of Science, C. Griswold; DEB–D.E. Bixler (pers. collection); MCZ–Museum of Comparative Zoology, H. Levi; RSV–R.S. Vetter (pers. collection); TRP–T.R. Prentice (pers. collection); UCR–Entomology Museum, University of California–Riverside; WRI–W.R. Icenogle (pers. collection).

### *Callobius guachama* Leech Figures 1–6

*Callobius guachama* Leech 1972: 53, figs. 84a, b, ♂. Male holotype from San Bernardino [San Bernardino County], California, in AMNH, examined.

**Diagnosis.**—*Callobius guachama* can be separated from other species of *Callobius* Chamberlin 1947 (except *C. nevadensis* (Simon 1884) and *C. severus* (Simon 1884)) by its larger size and from all species by genitalic differences. Mature specimens of *C. guachama* are consistently large whereas other *Callobius* species (e.g., *nevadensis*, *severus*, *pictus* (Simon) 1884 and *C. arizonicus* (Chamberlin & Ivie 1947)) may only occasion-

ally attain this size; most are medium-sized (10–13 mm) spiders (Leech 1972).

The males of *C. guachama* have the largest median apophysis (>1 mm) of any *Callobius* currently known, whereas median apophyses in both *C. nevadensis* and *C. severus* are 0.9. Additionally, the median apophysis in *C. guachama* has two distinct, subequal, well-rounded notches, whereas in *C. nevadensis* the anterior notch is much smaller than the posterior and in *C. severus* notches are not rounded and are poorly defined with an indistinct cusp when evident.

The female of *C. guachama* can be distinguished from all other *Callobius* species except *C. severus* by having a diminutive posterior lobe and from *C. severus* by having ectal margins of lateral lobes (posterior view) that are very robust and not broadly excavated.

**Description.**—*Male*: Overall length, 11–15, cephalothorax, 6.6–8.2 length, 4.4–5.7 width (at Leg III). Length of median apophysis, 1.00–1.22. In preserved specimens, abdomen varies in coloration from gray-to-brown and cephalothorax is sometimes uniformly orange, lacking the cephalic darkening noticed in the holotype and some of our specimens. The male palp is shown in Figs. 1, 2. Considering the diagnostic characteristics of palpal tibia and median apophysis, the male structures were consistent in their appearance with minor variation in size. The median apophysis consistently had two well-rounded notches of equal depth, the width of the anterior notch being slightly smaller than the posterior and a pointed cusp rising up to separate them.

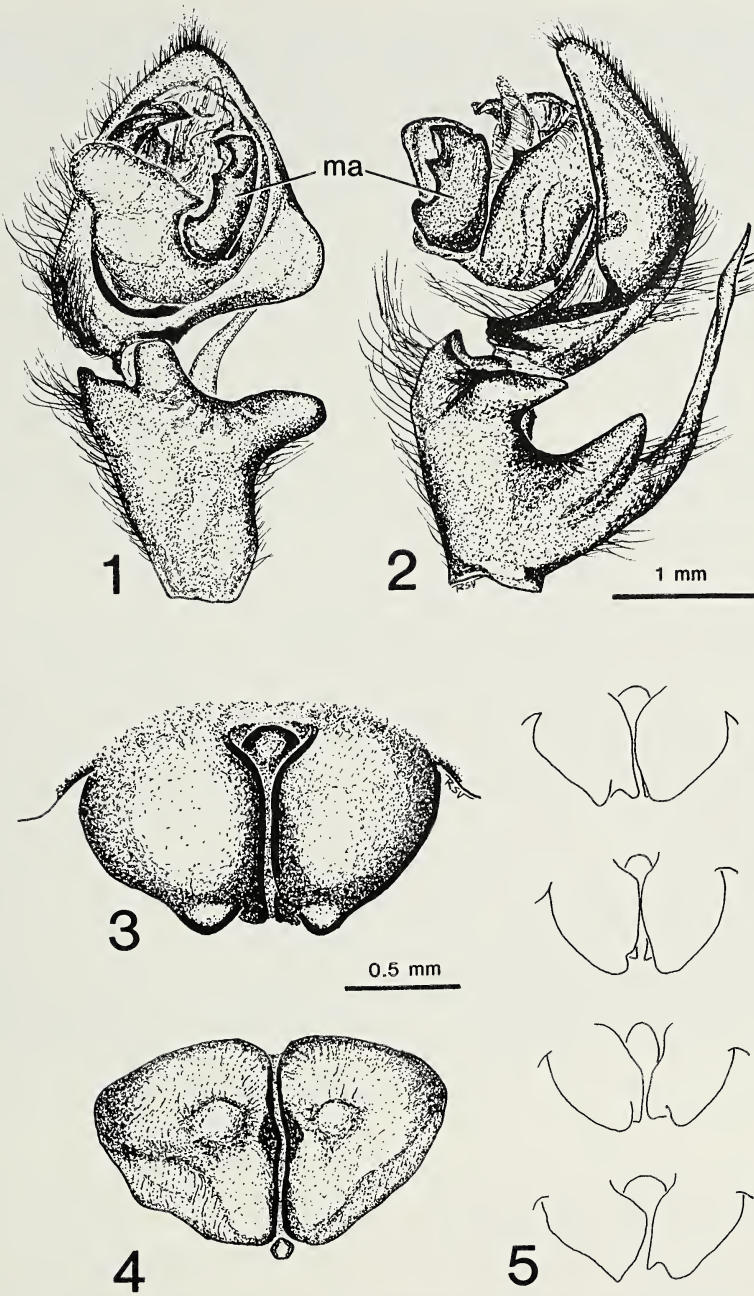
*Female*: Overall length, 15–20, cephalothorax, 7.0–8.4 length, 4.7–6.2 width. Epigynum, width, 1.4–1.74, measured across epigynum at the point where anterior margins of the lateral lobe intersect the transverse ectal margins. Color of legs and carapace usually light to dark chestnut, less often yellow-brown, cephalic region darker especially in subadults and adults; chelicerae dark usually appearing black; maxillae and labium also dark; tarsus of palp darker than proximal segments; abdomen usually dark grey with 2–3 pairs of faint, sometimes indistinguishable anterodorsal light orange-tan markings, most anterior pair usually appearing as longitudinal bands extending posteriad from anterior margin, 2nd

and 3rd pair usually subcircular corresponding to the dimples of muscle-impressions; venter dark, similar to carapace except light yellowish or tan regions of book lungs.

The epigyna (ventral view) with round-to-ovoid median lobe, lateral lobes as long as wide or slightly longer than wide, ectal lobes lacking and posterior lobe diminutive (posterior view), round-to-pentagonal in shape, width approximately  $\frac{1}{7}$  width of lateral lobe (Figs. 3, 4). Epigynum highly variable, asymmetrical in about half of specimens examined (total = 22, 6 slightly asymmetric, 6 very asymmetric). The posteriad protuberances on the lateral lobes contiguous with the posterior marginal line of the lateral lobe or protruded noticeably beyond. However, consistencies were noted in the diminutive posterior lobe and the robust nature of the lateral lobes in posterior view (Fig. 4). Outlines of epigyna are presented in Fig. 5 to show both variation and asymmetry.

**Material examined.**—Holotype male (AMNH), 25♂22♀26 imm. **CALIFORNIA:** Kern County, Tehachapi Mts., Paradise Valley (elev. 5000 ft.), 18 May 1960, 5 June 1960, in house, 2♂, W. Icenogle (WRI). Los Angeles County, San Gabriel Mts. (elev. 4800 ft.), Glendora Ridge, 4 August 1994, under road culvert, 1♀, T. Prentice (TRP); Soldier Creek (elev. 3740 ft.), 11 August 1994, 1imm.♀, T. Prentice (TRP). Riverside County, San Jacinto Mts., Idyllwild (elev. 5400 ft.), 24 June 1969, 1♂, H.E. Brown (UCR); late November 1996, in house, 1♀, C. Hamilton (RSV). San Bernardino County, San Bernardino (elev. 1150 ft.), 1 July 1969, in house, 1♂ (holotype), R. Miller (AMNH); San Bernardino Mts., Big Bear Lake (elev. 6750 ft.), 13 May 1994, in house, 1♂; 4 June 1994, in house, 1♀, N. Kohl (RSV); 29 August 1994, 1♀ (RSV); no date, 1♂ (RSV); 30 June 1995, 1♂ (RSV); 26 July 1995, in house in web in ceiling corner, 1♀, A. Sayles (RSV); 24 October 1995, in home on staircase 0300 h, 1♀, J. Reisman (RSV); early June 1996, in home in web, 1♂, J. Castiglioni (RSV); Crestline (elev. 5200 ft.), 29 May 1996, on bedroom ceiling, 1♂, K. McKinley (RSV); Fish Creek (elev. 6550 ft.), 8 June 1995, under bark, 3♀, T. Prentice (TRP); Forest Falls (elev. 7000 ft.), 17 May 1987, in house, 1♂ (DEB); Lake Arrowhead (elev. 5000 ft.), 30 April 1991, in cabin, 1♀, M. Laurich (BRH), 13 June 1995, in house,





Figures 1–5.—*Callobius guachama* Leech. 1, Male left palp, ventral view. 2, Left Palp, lateral view. *ma* = median apophysis. 3, Epigynum, ventral view; 4, Epigynum, posterior view; 5, Outline of epigyna (ventral view) showing variation and asymmetry.

1♂, P. Kimble (RSV); Lost Creek (elev. 7400 ft.), 17 May 1995, under fir stump, 200 ft. from creek, 1♀, T. Prentice (TRP); Mountain Home Creek, E. fork (elev. 5000 ft.), 29 March 1995, 2♂ 1♀ 4imm, 26 April 1995, 2♀, T. Prentice (TRP); Running Springs (elev.

6050 ft.), June 1994, in house, 1♂ (RSV); 6 June 1995, 2♂ 1penult♀ (RSV); 28 July 1995, in house, 1♀, S. Swinson (RSV); Santa Ana River (elev. 5500–6550 ft.), 15 November 1994, 1♀ 1penult♂; 30 March 1995, 1♂ 3imm♀; 10 May 1995, under bark of fir



Figure 6.—Geographical distribution of *Callobius guachama* (map from U.S. Geological Survey, Denver, Colorado).

tree, 2♀, T. Prentice (TRP); Seven Oaks (elev. 5600 ft.), 5 May 1996, under garbage can, under bark, 4imm, 17–19 May 1996, under loose bark of fallen pine trees, 2♂1♀12imm, R. Vetter (RSV); Sugarloaf (elev. 7050 ft.), 27 June 1995, in kitchen sink, 1♀, 3 July 1995, in bathroom, 1♂, K. Vargas (RSV); Twin Peaks (elev. 5400 ft.), no date, 1♂, W. Sears (UCR), 22 April 1996, in bathroom, 1penult♂, 23 May 1996, in toy chest, 1♂, C. Wormald (RSV); June–July 1996, under trash, 3imm, K. Wormald (RSV); 13 July 1996, in house, 1♂, C. Hinkleman (RSV).

We have deposited several specimens of each sex at both AMNH and CAS. Most of

the remainder are deposited at UCR or TRP collections.

## DISCUSSION

*Callobius guachama* is a montane spider found in southern California from 1150–2250 m elevation on at least four mountain ranges (San Jacinto, San Bernardino, San Gabriel and Tehachapi; Fig. 6). The last three of these ranges are contiguous, while the more southern San Jacinto mountains are separated from the nearby San Bernardino mountains by a narrow pass of 600 m elevation.

In contrast to the other specimens we obtained in this study, the holotype male was



described from the densely-populated urban area (Norton Air Force Base, elev. 300 m) near the foothills of the San Bernardino mountains. All specimens presented to us by the public have come from the sparsely-populated mountain communities. If *C. guachama* does live in the lowlands, it is surprising to us that more specimens have not been turned in to authorities for identification. It appears possible that the holotype may have been transported from an area of higher elevation to its collection site.

*Callobius guachama* is found in natural rock outcroppings, under bark of dead fir and pine trees, in deep crevices of living cedar, pine and fir or in human-altered environments such as under road culverts and highway underpasses. It also is occasionally discovered in domiciles in the mountain communities, at times causing great alarm to the human inhabitants who fear that this large spider is dangerous. Most *C. guachama* males in this study were found in homes (probably searching for mates) and were subsequently destructively captured and brought in for identification, but a few females were also similarly collected. Most of the spiders collected by the lay community were found in the warm months of May–August, with one female being taken in a house in late November; our field-collected spiders were taken from late March to November. The areas in which these spiders have been collected have winter temperatures routinely below 0 °C with extended periods of snow cover (some of these locales are popular winter tourism areas). *Callobius guachama* has been active when temperatures were as low as 8 °C; one spider was taken at dawn while it crawled on a wall in an unheated campground washroom.

Using the *Callobius* key provided in Leech (1972), all of the males in this study emerge as *guachama*. Females of *C. guachama* uniformly can be keyed out to having two ventral (4 total) spines distally located on metatarsi I and II (couplet 25b) and usually 3 or 4 spines proximally on metatarsi I and II (couplet 40a) although some had 1 or 2 metatarsi with as few as 2 and as many as 6 spines. From this point, the posterior lobe of the epigynum is diminutive which would key out to *C. severus* (couplet 41b; one of two times the female of

this species emerges in the key). (We use here the term “diminutive” whereas Leech used the term “vestigial”. As a reviewer correctly pointed out, this latter term denotes an evolutionary derivation of a structure once functional). One might amend the key to incorporate the female of *C. guachama* by adding at this point, “in posterior view, diminutive posterior lobe with robust lateral lobes”.

Finally, because of the depauperate *Callobius* fauna in southern California, we investigated the possibility that the holotype of *Auximus pallescens* Chamberlin 1919 might be an immature of *C. guachama*. *Auximus pallescens* was named on the basis of an immature female collected in Claremont near the foothills of the San Gabriel mountain range (Chamberlin 1919); it was synonymized with *C. nevadensis* by Leech (1972). We have examined this holotype as well as the four known *C. nevadensis* specimens (all mature females; three from AMNH, one from DEB) from the Los Angeles Basin and are satisfied that the holotype is not an immature of *C. guachama* and, therefore, no taxonomic name change needs to be made.

#### ACKNOWLEDGMENTS

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## FORAGING VERSATILITY AND THE INFLUENCE OF HOST AVAILABILITY IN *ARGYRODES TRIGONUM* (ARANEAE, THERIDIIDAE)

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**ABSTRACT.** *Argyroides trigonum* (Hentz 1850) can interact with its host as kleptoparasite, host predator, web-stealer, or commensal. This species can also capture insect prey in a web of its own construction. Which foraging strategy an individual *A. trigonum* exhibits certainly depends on a multitude of environmental factors, especially host availability. In this study, field surveys of populations of *A. trigonum* and its hosts and daily observations of individually marked host webs were made at sites in Ohio and New Hampshire. These observations together with a manipulation of *A. trigonum* density were performed in order to determine the influence of host species and abundance on the foraging strategy of *A. trigonum*. *A. trigonum* utilized *Neriene radiata* (Walckenaer 1841) to a greater extent than alternative hosts at both web sites even though many other host species were more abundant. The percentage of *A. trigonum* sharing a web with the host did not change with differing host/*A. trigonum* ratios; however, as a host/*A. trigonum* ratio increased, more *A. trigonum* were found in unoccupied host webs and fewer *A. trigonum* were found in webs of their own construction. *A. trigonum* is more likely to share a web with *Pityohyphantes costatus* (Hentz 1850) and to usurp the webs of *Neriene radiata*. Overall, *A. trigonum* behaved predominantly as a host predator; however, kleptoparasitism is more likely in host webs that last longer. Capturing prey in self-constructed or empty host webs is also important to *A. trigonum* foraging.

While some species utilize only one or a narrow set of behaviors to accomplish a certain task such as acquiring food, others exhibit a broad repertoire of behavioral strategies to achieve the same goal. Such behavioral versatility in a population could be the result of phenotypic plasticity of individuals responding to a variety of environmental pressures, genetic differences among individuals within a population, or both. Although some species of spiders are known to be quite versatile in their behavior (Jackson & Hallas 1986; Jackson & Poulsen 1990), very little research has been done to determine the correspondence between alternative behavioral strategies and their possible associated environmental factors.

The spider genus *Argyroides* Simon 1864 (family Theridiidae) is commonly thought to be comprised of species that forage primarily by invading the webs of other host spiders and kleptoparasitizing their captured prey, or behaving as commensals in host webs. However, some species have also been shown to be predators of their hosts (Exline & Levi 1962;

Smith-Trail 1980; Wise 1982; Tanaka 1984; Larcher & Wise 1985; Whitehouse 1986; Suter et al. 1989). According to Whitehouse (1986, 1987), those species that appear to be exclusively araneophages (or host predators) are members of the sub-genera *Rhomphaea* (L. Koch 1872) or *Ariamnes* (Thorell 1870), which may actually be genera distinct from *Argyroides* (although closely related). In fact, many species of *Argyroides* are both kleptoparasitic and araneophagic (Whitehouse 1986), and the foraging behavior of few species has been studied in enough detail to determine the full range of their foraging possibilities (but see Vollrath 1979a, b: *A. elevatus* Taczanowski 1873; Whitehouse 1986, 1988, 1993: *A. antipodiana* Cambridge 1880; and Cangialosi 1990, 1991: *A. ululans* Cambridge 1880). Work by Larcher & Wise (1985) and Cangialosi (unpubl. data) indicates that *Argyroides trigonum* (Hentz) utilizes an array of foraging tactics including kleptoparasitizing prey from a host web, using an occupied or unoccupied host web to capture its own prey, preying on the host spider, and cap-



turing insect prey in a web of its own construction. Elucidating the factors responsible for foraging versatility in *A. trigonum* should further our understanding of the ways in which the environment may or may not influence behavior.

Although many factors are probably influential in determining which foraging strategy is exhibited by an individual *A. trigonum*, the availability of hosts is presumably one of the most important. The major objectives of this investigation were to determine the diversity of host species utilized by *A. trigonum*, the relative importance of each of the different foraging modes it exhibits, and how foraging mode is influenced by host species and host abundance. In particular, I hypothesize that 1) changes in host abundance cause shifts in the percentages of *A. trigonum* exhibiting different foraging strategies, and 2) *A. trigonum* uses different foraging tactics when interacting with the host species, *Neriene radiata* Walckenaer (family Linyphiidae) than it does when interacting with the host species, *Pityohyphantes costatus* Hentz (family Linyphiidae). These two host species were selected for comparison because both are major hosts for *A. trigonum*, and differences between them in web structure and body size was expected to provide different foraging challenges for *A. trigonum*.

## METHODS

**Study sites.**—Two study sites were used for data collection and comparison. One site was the forested portion of Miami University's Ecological Research Center in Oxford (Butler County), Ohio. The other was the Greater Goose Pond Forest in Keene (Cheshire County), New Hampshire. Both of these sites are temperate deciduous forest although the Keene site has a greater proportion of coniferous trees, especially white pine and hemlock. *Argyodes trigonum* and its hosts are common in the understory of both forests.

**Study species.**—*Argyodes trigonum* is common throughout the eastern portions of Canada (Ontario), and the United States from central Wisconsin to eastern Texas, and Maine to Florida (Exline & Levi 1962). The body length of adults ranges from approximately 2–4 mm. When not in a host web, *A. trigonum* builds a very small tangle web or hangs from just a few strands of silk. The two host species

used in the individual web observations, *Neriene radiata* and *Pityohyphantes costatus*, are both linyphiids. *Neriene radiata* builds a dome-shaped sheet web with barrier silk extending above the dome. The spider usually sits just beneath the central area of the dome. *Pityohyphantes costatus* builds a hammock-shaped triangular sheet which is flatter and longer than that of *N. radiata*. Barrier silk also extends above the sheet of *P. costatus*. *Pityohyphantes costatus* builds a retreat which usually consists of dense silk placed in a rolled leaf or under a piece of tree bark at one end of the sheet. The spider is often found within this retreat, or underneath the central part of its sheet web.

**Ohio site field survey.**—To gain some measure of overall host use by *A. trigonum* in this study site, a 20 × 2 m plot of forest was censused weekly from August–October 1990 for a total of 11 weeks. The number of web-building spiders of all species (if easily identified) or family present was recorded. I also recorded the presence of *A. trigonum* in a web with a host, in a host web alone, or in a web of its own construction. Then, the number of host spiders relative to the number of *A. trigonum* (host/*A. trigonum* ratio) was calculated for each date. The percentage of *A. trigonum* observed in each of the three above situations was plotted against host/*A. trigonum* ratio for all 11 dates and Spearman Correlation Coefficients were calculated.

**New Hampshire site host/*Argyodes* ratio manipulation.**—In the forests of New Hampshire, it is common to find short walls of piled stones (mostly granite) that were used as property dividers 100 or more years ago. Many understory spiders build webs on these rocks and the vegetation that grows between and around the rocks. I utilized one of these walls as a convenient way to define control and manipulated areas. The wall used was approximately 0.75 m high. Three areas along the wall, each 10 m in length and 1.5 m in width, were marked at the edges with painted tent stakes and randomly designated as control, removal or addition. The three areas were separated by approximately 40–50 m of stone wall that was ignored in this study. In order to create a wide range of host/*Argyodes* ratios, I manipulated *A. trigonum* density in two of the three areas. I removed all *A. trigonum* from the removal area beginning on 13 July

Table 1.—*Argyrodes trigonum* utilization of host webs at the New Hampshire and Ohio study sites. "With *A. trigonum*" indicates web sharing. (arg = *A. trigonum*). Data are from the control area of the NH site density manipulation and the Ohio site field survey.

Host spider	New Hampshire				Ohio			
	# of hosts alone	# with <i>A. trigonum</i>	% occupied webs with arg	# arg in host web alone	# of hosts alone	# with <i>A. trigonum</i>	% occupied webs with arg	# arg in host web alone
Linyphiidae								
<i>Neriene radiata</i>	471	16	3.3	44	277	30	9.8	92
<i>Frontinella pyramitela</i>	—	—	—	—	190	5	2.6	13
<i>Pityohyphantes costatus</i>	70	1	1.4	2	34	1	2.8	2
Other Linyphiidae	192	0	0	0	—	—	—	—
Theridiidae	782	0	0	0	—	—	—	—
Agelenidae	297	1	0.34	0	11	4	26.7	2
Orb Weavers	62	0	0	2	341	0	0	0

1993 and continuing every 1–2 days until 10 October 1993. *A. trigonum* were added to vegetation in the center of the addition area, but not directly in host webs, and kept at the level of 10–15 total individuals (checked every 1–2 days) in this same time period. The *A. trigonum* used for additions were those taken from the removal area as well as some spiders collected approximately two km away from the experimental areas. The control area was left alone.

The foraging situation of *A. trigonum* (sharing a web with host, in host web alone, or in self constructed web) was recorded for all individuals within the three areas every 1–2 days. Number of hosts and *A. trigonum* were also recorded in each of the three areas and the host/*A. trigonum* ratio was calculated for each observation date. The number of *A. trigonum* in the removal area was not zero because of continuous immigration of *A. trigonum* into this area. Observation of their foraging situation was made just before removal. As with the Ohio data, the percentage of *A. trigonum* observed in each of the three above situations was plotted against weekly host/*A. trigonum* ratio and Spearman Correlation Coefficients were calculated. (Weekly, instead of daily, ratios were used in order to make more direct comparisons with the Ohio data. I used the ratio for the first day of the week that counts were recorded). Because a wider range of host/*A. trigonum* ratio was exhibited in these manipulated areas compared to the Ohio site, two sets of Spearman correlations were performed for the New Hamp-

shire data: one for host/*A. trigonum* ratios of less than 6:1 (for comparison with the Ohio data), and another for all ratios. Additionally, the data from the control area was compared to the Ohio site field survey in order to compare overall host species utilization between the two sites (Table 1).

#### Observations of individual host webs.—

At the New Hampshire site, occupied webs of *Neriene radiata* and *Pityohyphantes costatus* were located and the web site and webs were individually marked by placing flagging on vegetation near the web and a twist tie at one edge of the web at its attachment to the vegetation. No spiders were marked. Observations of groups of 23–25 host-only occupied webs of each species were initiated on 15 June, 19 July, 9 August, and 26 August 1994, making a total of 94 *P. costatus* and 95 *N. radiata* webs that were observed. Each web was observed every day until the complete disappearance of the web. The following data were recorded: host was alone in its web, *A. trigonum* was alone in the host web, the host and *A. trigonum* were together in the web, the web was empty (no spiders), the web was destroyed or gone. If an *A. trigonum* invaded a host web, emigrated, and then another (or the same) *A. trigonum* invaded that web later, the host web was considered to be invaded twice. Because several host webs were invaded by *A. trigonum* more than once, the total number of observations beginning with a host alone in its web was 148 for *P. costatus*, and 107 for *N. radiata*.

I initially summarized these observations



by constructing an ethogram of all fates of host webs with respect to the invasion of *A. trigonum*. Then, frequency of transition (%) from one state to the next was calculated between all states (i.e., host alone, *Argyrodes* alone, *Argyrodes* and host together, etc.) for both host species. These frequencies were compared between the two host species using contingency table analysis for the following: the frequency of web sharing and web takeover, the outcome of web sharing (the frequency of *A. trigonum* emigration and host emigration); and the outcome of web takeover (the frequency of host reclaiming the web and *A. trigonum* emigration). Mean duration of web sharing and web takeover were compared between the two host species using Kruskal-Wallis tests.

I also calculated the frequency of empty web invasion by *A. trigonum*, and compared the persistence (mean duration) of empty webs invaded and not invaded by *A. trigonum* between host species by log-transforming the non-normally distributed data and then utilizing a 2-way ANOVA. Additionally, mean duration of occupied host webs was compared between host species with a Kruskal-Wallis test.

## RESULTS

**Host utilization.**—Data from the Ohio site field survey and the control area of the New Hampshire site density manipulation were used in Table 1 to compare overall host species/family utilization between these two sites. *A. trigonum* uses a variety of hosts; however, a preference for *Neriene radiata* was seen in both the New Hampshire and Ohio study sites. The percentage of *A. trigonum* observed sharing a web with *N. radiata* was 2–9× higher compared to most of the other hosts (Table 1). Also, the number of *A. trigonum* in empty webs (no host present) was 7–50× higher in the webs of *N. radiata* compared to the other host spiders. *A. trigonum* also made substantial use of *Frontinella pyramitela* (Walckenaer 1841)(family Linyphiidae) at the Ohio site, and *Pityohyphantes costatus* at both sites (Table 1). The number of agelenids in the study area at the Ohio site was only 11, but nearly a third of these were observed with an *A. trigonum* individual in their webs. Although there were several hundred agelenids, other linyphiids and theridiids observed at the New

Hampshire site, *A. trigonum* made little or no use of these hosts. Orb weavers were never observed sharing a web with *A. trigonum*, and only two empty orb webs contained an *A. trigonum* individual (Table 1).

**Host abundance and foraging mode.**—*A. trigonum* foraging mode was influenced by the relative number of hosts available in some cases in both the Ohio survey and the manipulation at the New Hampshire site. Due to the manipulation and the smaller area sizes, the range of host/*A. trigonum* ratios was much greater in the New Hampshire site (from 1.4:1 to 67:1 for New Hampshire, and all less than 5:1 in Ohio). There were no significant relationships between host/*A. trigonum* ratio and any of the three foraging situations at the New Hampshire site when the full range of ratios are included in the analyses. However, when host/*A. trigonum* ratios of less than 6:1 are considered, some patterns emerge that are similar to the Ohio site data.

At the Ohio site, the percentage of *A. trigonum* observed in a web of its own construction decreased significantly with an increase in the host/*A. trigonum* ratio (Spearman Coeff.  $R = -0.644$ ,  $P < 0.05$ , Fig. 1a). This same pattern was seen at the New Hampshire site (Spearman Coeff.  $R = -0.769$ ,  $P < 0.001$ , Fig. 1b). At the Ohio site, the percentage of *A. trigonum* observed in host webs alone increased significantly with an increase in the host/*A. trigonum* ratio (Spearman Coeff.  $R = 0.725$ ,  $P < 0.01$ , Fig. 1c). However, this relationship was not seen at the New Hampshire site (Spearman Coeff.  $R = 0.449$ ,  $P = 0.192$ , Fig. 1d). There was no relationship between the percentage of *A. trigonum* sharing a web with a host spider and the host/*A. trigonum* ratio at either site (Ohio: Spearman Coeff.  $R = -0.198$ ,  $P > 0.10$ , Fig. 1e; New Hampshire: Spearman Coeff.  $R = 0.056$ ,  $P > 0.5$ , Fig. 1f).

**Host species and foraging mode.**—The observations of *N. radiata* and *P. costatus* webs at the New Hampshire site revealed several sequences that took place with respect to the invasion of *A. trigonum* from the time that a host was first observed occupying its web alone until that web's demise. These sequences are summarized as a whole in Fig. 2 and subsets of this figure appear in Figs. 3, 4. Overall, a high percentage of host webs were invaded by *A. trigonum*. Of the total number

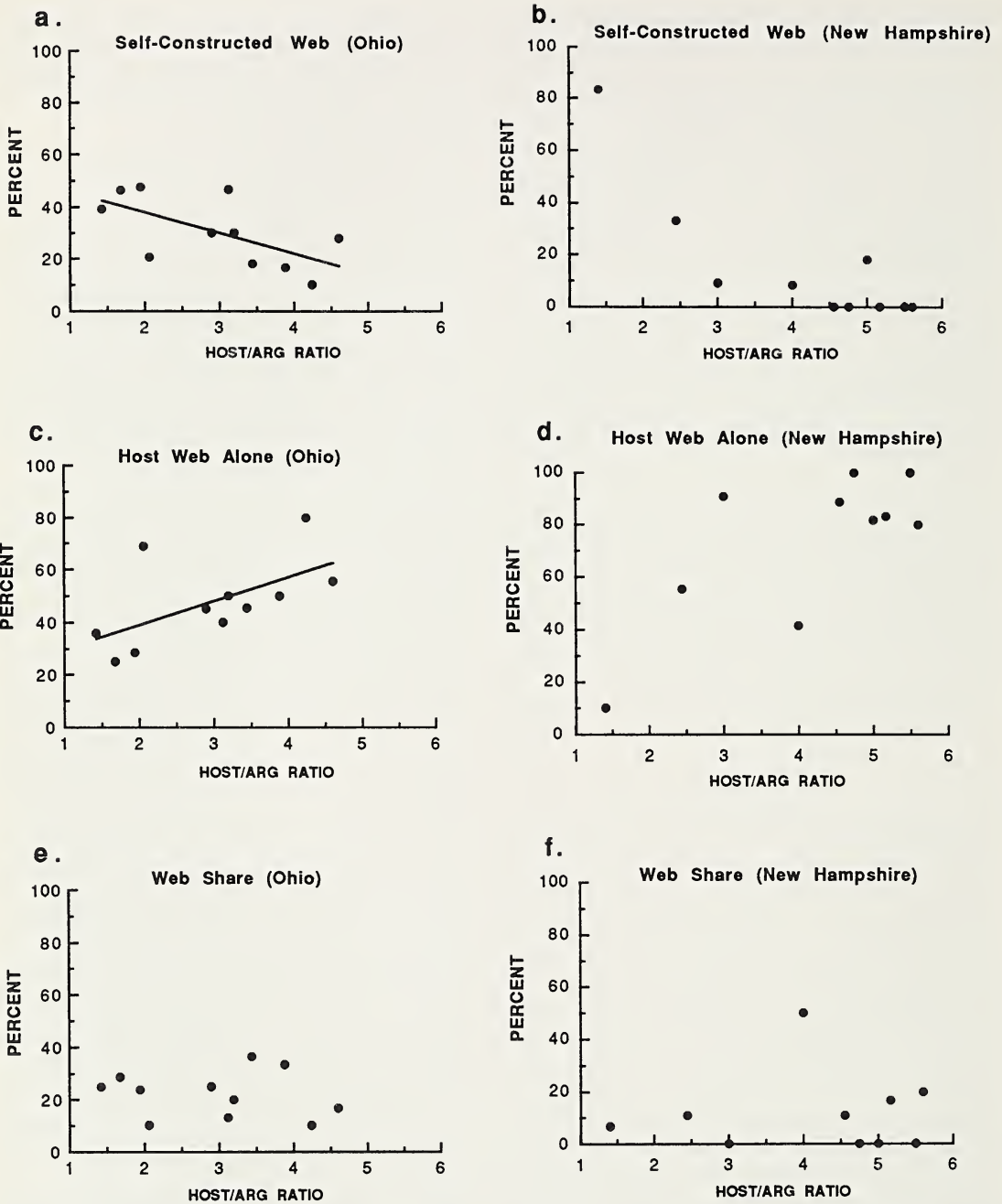


Figure 1.—Percentage of *Argyrodes trigonum* found in unoccupied host webs (host web alone), occupied host webs (web share), or in self-constructed webs, compared to relative host abundance for the Ohio survey (a, c, e) and the New Hampshire density manipulation (b, d, f). ARG = *Argyrodes trigonum*.

of observations beginning with a host alone in its web, 45.9% of *P. costatus* webs and 54.2% of *N. radiata* webs were invaded by *A. trigonum* (Fig. 3). There were 30 webs that were invaded more than once. For *P. costatus*,

17 webs were invaded twice, three webs were invaded three times, and one web was invaded four times. For *N. radiata*, seven webs were invaded twice and two webs were invaded three times.



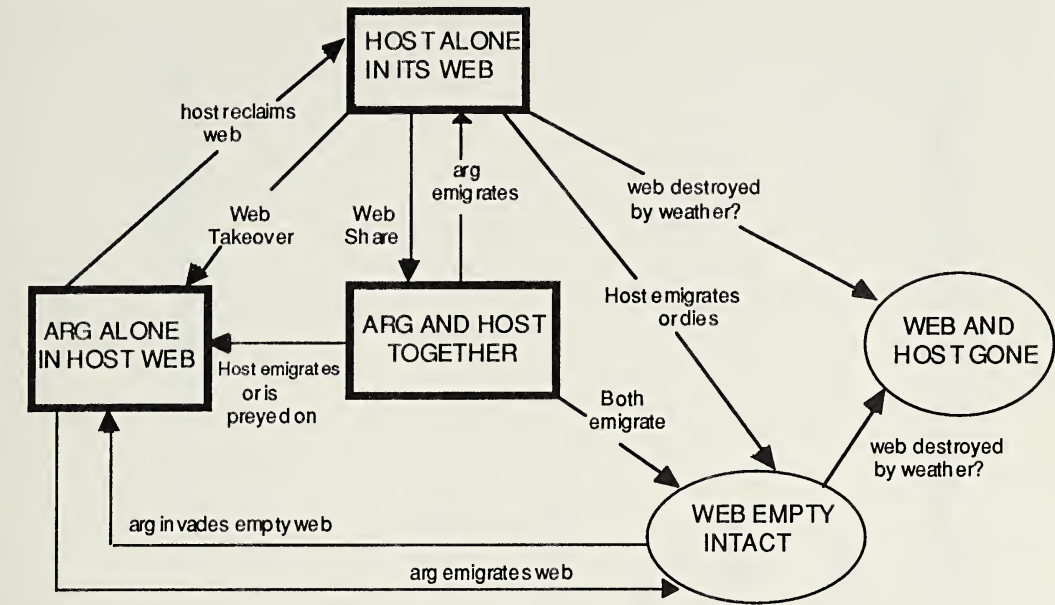


Figure 2.—Fates of host occupied, *Argyrodes trigonum* occupied, both occupied, and empty webs for individual webs observed at the New Hampshire site. (This figure can be compared to Figs. 3 & 4 to determine percentage outcome for observations beginning with the rectangular boxes.)

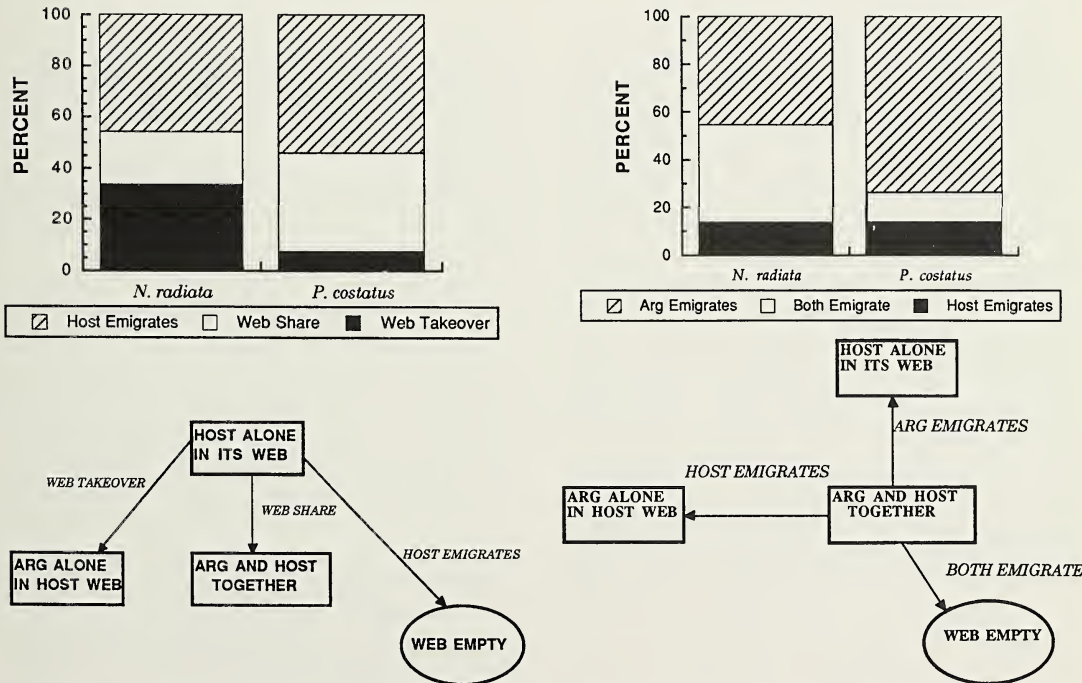


Figure 3.—The percentage of total host-only occupied webs that were either taken over by an *Argyrodes trigonum*, shared with an *Argyrodes trigonum*, or host emigrated/web destroyed for both *Neriere radiata* ( $n = 107$ ) and *Pityohyphantes costatus* ( $n = 148$ ) webs ( $\chi^2 = 30.97$ ,  $P < 0.0001$ ).

Figure 4.—Web sharing outcome. The percentage of host and *Argyrodes trigonum* occupied webs that resulted in *Argyrodes trigonum* emigration, host emigration, or both emigrating for both *Neriere radiata* ( $n = 22$ ) and *Pityohyphantes costatus* ( $n = 57$ ) webs ( $\chi^2 = 7.73$ ,  $P < 0.05$ ).

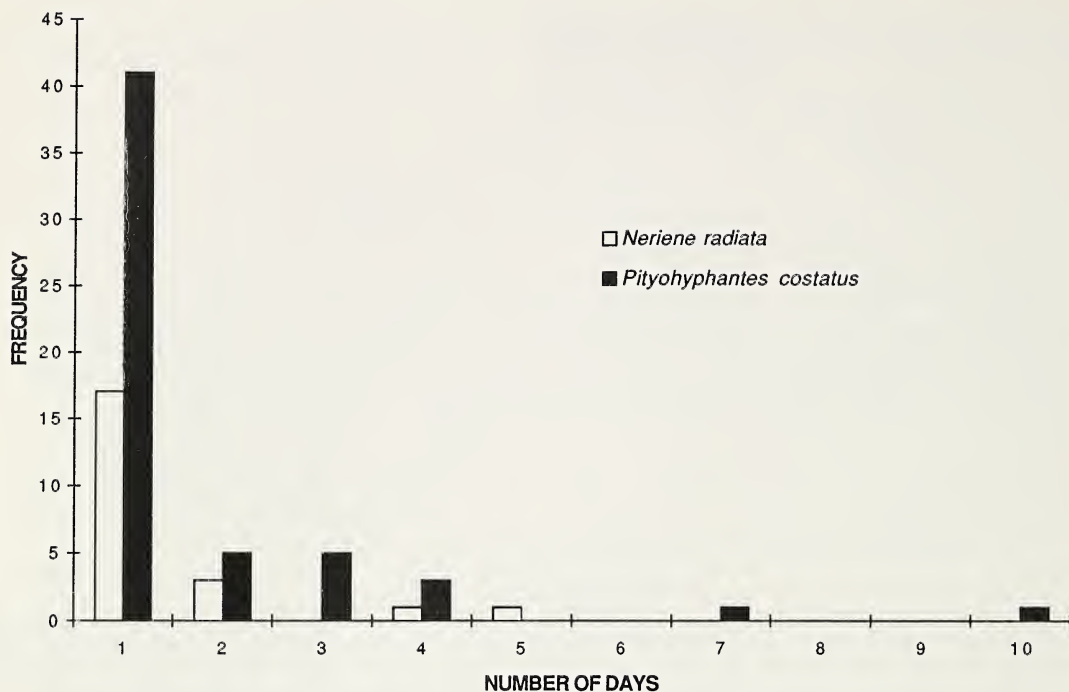


Figure 5.—Web sharing time. Frequency distribution of time (days) *Argyrodes trigonum* spent in occupied host webs for both host species.

*Web sharing vs. web takeover:* In order for *A. trigonum* to eventually usurp a host's web, there must be some period of co-occupation of the web with that host. Web takeover here refers to an *A. trigonum* individual observed to be alone in a host web within 24 h of that web having been observed with the host as the sole occupant, while web sharing refers to the host and *A. trigonum* co-occupying the web for at least 24 h. The invasion of occupied host webs by *A. trigonum* more frequently resulted in web takeover for *N. radiata* and in web sharing for *P. costatus* ( $\chi^2 = 30.97$ ,  $P < 0.0001$ , Figs. 2, 3). Web takeover may indicate either host predation or web stealing (through forced host emigration). Although webs generally were not observed for more than a few minutes on each day, I did observe direct evidence of host predation on several occasions. There were four observations of *N. radiata* being fed on by *A. trigonum*, or a dead *N. radiata* in the web next to an *A. trigonum*, and one observation of *A. trigonum* feeding on *P. costatus*. All of these webs had a hole torn in the dome or sheet approximately 2–4 cm in diameter. Most of the host webs that were seized by *A. trigonum* were observed

with large holes in the dome or sheet portion of the web. I also observed the host being chased off its web by *A. trigonum* a total of two times, once for each of the two host species. The reverse situation was observed once when an *A. trigonum* individual was chased off the host web by *P. costatus*.

*Outcome and duration of web sharing:* There was a significantly higher proportion of *A. trigonum* only emigrating from *P. costatus* webs, and a significantly higher proportion of both host and *A. trigonum* emigrating from *N. radiata* webs after a period of web sharing ( $\chi^2 = 7.73$ ,  $P < 0.05$ , Figs. 2, 4). There was no difference between the two host species in the frequency of the host giving up the web and leaving *A. trigonum* alone after web sharing occurred. Also, mean duration of web sharing was not significantly different for *P. costatus* compared to *N. radiata* (Kruskal-Wallis:  $\chi^2 = 0.195$ ,  $P = 0.659$ , Fig. 5). Whereas web sharing never lasted longer than five days for *N. radiata*, there were two observations of web sharing for *P. costatus* that continued for a greater period of time than this, one for seven days and one for 10 days (Fig. 5).

*Outcome and duration of web takeover:*



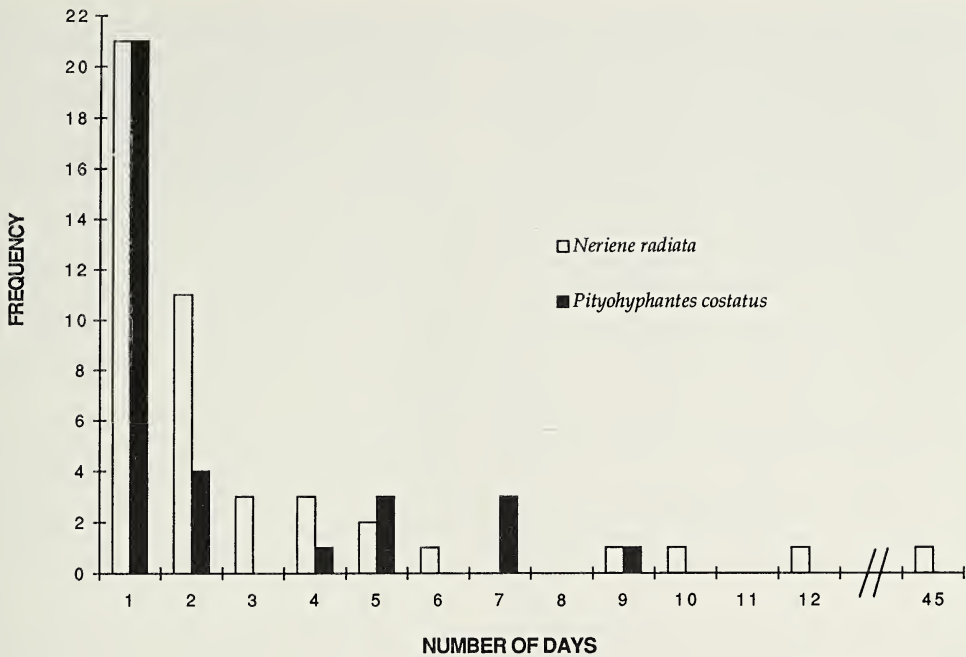


Figure 6.—Time alone in host web. Frequency distribution of time (days) *Argyrodes trigonum* spent in unoccupied host webs for both host species.

Once an *A. trigonum* had become sole occupant of a host web, the likelihood of a host regaining control of that web was small for both host species (less than 10% of webs). The percentage of webs reclaimed by host spiders after being usurped by *A. trigonum*, was not significantly different between *P. costatus* and *N. radiata* ( $\chi^2 = 1.34$ ,  $P > 0.24$ ). The mean duration of *A. trigonum* alone in a host web was not significantly different for the two types of host webs (Kruskal-Wallis:  $\chi^2 = 1.17$ ,  $P = 0.278$ , Fig. 6). The longest periods of time that an *A. trigonum* spent alone in a host web were in *N. radiata* webs. There were three observations of an *A. trigonum* spending 10, 12, and 45 days alone in a *N. radiata* web (Fig. 6).

Table 2.—ANOVA for mean duration (log-transformed) of empty host webs invaded and not invaded by *Argyrodes trigonum*.

Source	df	Sum of squares	F-ratio	P > F
Host species	1	0.621	6.722	0.010
Invasion	1	1.665	18.023	<0.0001
Species $\times$ invasion	1	0.030	0.326	0.568

**Persistence of occupied and unoccupied webs.**—The average time beginning with a host first observed in its web until the host was gone, was significantly greater for *P. costatus* (*P. costatus*: mean  $\pm$  SE =  $9.74 \pm 1.15$  days,  $n = 70$ ; *N. radiata*: mean  $\pm$  SE =  $3.74 \pm 0.63$  days,  $n = 46$ ; Kruskal-Wallis:  $\chi^2 = 13.77$ ,  $P < 0.001$ ). Host webs that became devoid of a host spider (empty) were sometimes invaded by *A. trigonum*. For *P. costatus*, 19.4% (18 out of 93) of empty webs were invaded by *A. trigonum* compared to 9.2% (8 out of 87) of empty *N. radiata* webs. The persistence of a web without its host spider was significantly longer for those webs that were invaded by *A. trigonum* compared to webs that were never invaded (Table 2). As with occupied webs, empty *P. costatus* webs lasted significantly longer than *N. radiata* webs (Table 2).

DISCUSSION

Vollrath (1984) classified species of *Argyrodes* as either generalists or specialists, where generalists are those species that utilize a wide variety of hosts from different families, and specialists are restricted to one or a few host species. Whitehouse (1988) added that

generalists use only a few techniques to obtain food, while specialists utilize several techniques. However, a host generalist might be expected to need a wider scope of foraging techniques in order to deal with hosts of differing size, defensive ability, and web type. *A. trigonum* appears to be a generalist in both senses as it uses a variety of hosts and a variety of foraging strategies.

Although *A. trigonum* utilized several types of hosts at both the Ohio and New Hampshire sites, its presence in the webs of hosts was not in proportion to the number of those hosts or host webs available. Even as a generalist, *A. trigonum* shows a preference for certain host types which were mainly linyphiids at these study sites. The eleven agelenid webs at the Ohio site were large (about 30 cm in diameter) and provided an extensive amount of barrier webbing which might explain the extremely high percentage of *A. trigonum* in their webs. The agelenids, theridiids, and other linyphiids at the New Hampshire site were mostly juveniles within the time period of this study, tended to have little barrier silk, and built their webs deep in the small spaces between the rocks. These characteristics likely made these hosts less accessible or functional to *A. trigonum*. Overall, the number of *A. trigonum* at the New Hampshire site was low compared to the Ohio site, especially considering that a greater number of webs at the New Hampshire site were surveyed. In this study, *A. trigonum* made virtually no use of orb weavers. At a site in Maryland, *A. trigonum* is found often in the webs of the orb weaver, *Metepeira labyrinthea* Hentz 1847 (family Araneidae) (Wise 1982; Larcher & Wise 1985). Orb weavers in this genus build a barrier web in addition to the orb whereas most others do not. I have never observed *M. labyrinthea* at the New Hampshire site, and have only seen a few individuals at the Ohio site in the course of several years. Although *A. trigonum* exhibits preferences for certain hosts when choices are available, its ability to utilize many different hosts may be largely responsible for its wide geographical distribution.

In this study, *A. trigonum* was observed occupying the web of a host that is no longer present, occupying the web of a host that is present (web sharing), and occupying a self-constructed web. Changes in relative host abundance influence *A. trigonum* foraging

mode to a certain extent by altering the percentage of *A. trigonum* found in these three situations. However, determining precisely how individuals shift their mode of foraging is difficult because these situations indicate a complexity of foraging alternatives (Table 3). Also, foraging is certainly influenced by a variety of other factors. The abundance data together with the observations of individual host webs reveals more about the relative extent to which *A. trigonum* behaves as a kleptoparasite, predator, web stealer, or independent forager.

Several pieces of evidence indicate that *A. trigonum* behaves as a spider predator or web stealer to a greater extent than a kleptoparasite in these two study areas. More *A. trigonum* were observed in unoccupied host webs than in occupied host webs at both the Ohio and New Hampshire sites. Also, there was a higher percentage of *A. trigonum* in unoccupied host webs than in either of the other two situations (in occupied host webs, in self-constructed webs) in all three of the areas in the manipulation (addition, removal, control). Because the percentage of total hosts at any one time with *A. trigonum* in their webs was fairly low (about 1–10%), and the percentage of observed webs that eventually were invaded by *A. trigonum* was high (45.9–54.2%), it seems that relatively few *A. trigonum* move around quite frequently and eventually invade a large portion of the available webs. This high mobility in general is more consistent with a predatory or web-stealing as opposed to a kleptoparasitic lifestyle. The direct observations of host predation support this claim as well.

In spite of the largely predatory nature of *A. trigonum*, the importance of prey kleptoparasitism cannot be ruled out. About 20% of *A. trigonum* both in the manipulation in New Hampshire and in the Ohio survey were consistently observed in an occupied host web (web sharing), regardless of host density. In comparing the two host species, web sharing occurred more frequently with *P. costatus* whereas web takeover was more likely with *N. radiata*. This is probably related to the fact that occupied *P. costatus* webs last longer than *N. radiata* webs and provide a greater amount of barrier silk. Host size (Larcher & Wise 1985) and defensive behavior are also important. *P. costatus* is somewhat larger and



Table 3.—Three major situations in which an *Argyrodes trigonum* individual can be found in relation to a host and the modes of foraging and access to foraging sites that these situations indicate.

<i>Argyrodes trigonum</i> /host web situation	<i>Argyrodes trigonum</i> foraging modes and access to foraging sites
Occupy host web alone	1) has preyed on the host (host predator) 2) has caused the host to emigrate and is using the host web for insect prey capture (web stealer) 3) has invaded an empty host web and is using it for insect prey capture (web scavenger)
Share web with host	1) is taking insect prey unimportant to the host (commensal) 2) is taking insect prey important to the host (kleptoparasite) 3) is in a temporary transition stage to steal host web or prey on the host
In self-constructed web	1) is foraging for insect prey (independent forager) 2) is in the process of host web location

usually resides in a retreat at the edge of its web under bark or in a rolled leaf. This may explain why a greater percentage of *A. trigonum* emigrated from *P. costatus* webs compared to *N. radiata* webs leaving the host alone again after a period of sharing. Larcher & Wise (1985) also found that the probability and duration of web sharing was different for different host species. *Metepeira labyrinthea* were less likely to abandon their webs when invaded by *A. trigonum* compared to *N. radiata*, although *A. trigonum* did prey on *M. labyrinthea* at a substantial rate. In general, it seems reasonable to assume that in areas which are dominated by larger host species with long lasting webs and a large amount of barrier or tangle silk, and perhaps reside in retreats (e.g., large agelenids, theridiids such as *Achaearanea tepidariorum* C.L. Koch 1841), *A. trigonum* will behave predominately as kleptoparasites or commensals.

The significance of capture of their own insect prey by *Argyrodes* (whether by use of a host web or a self-constructed web) as a way of obtaining food, has been minimized or ignored by most workers. Vollrath (1984), in his review of kleptobiotic interactions in invertebrates, even states: “no *Argyrodes* is known to construct and operate a feeding web”. However, Eberhard (1979) described in detail the use of a self-constructed web by *A. attenuatus* in order to capture prey which included not only spiders but a large proportion of insects. Although this web differs from the typ-

ical theridiid snare, it is used as a substrate for the capture of insect and spider prey and could therefore be considered a capture web. *A. antipodiana* will attack and subdue flies on both its own and the host’s web (Whitehouse 1986). I have observed *A. trigonum* capture and feed on insects on a self-constructed web both in the laboratory and in the field (unpubl. obs.). Larcher & Wise (1985) showed that *A. trigonum* captured more than 50% of the insects that they introduced into host unoccupied webs. In this study, there was always at least 15%, and up to 40%, of the total population (at both sites) that were found in webs of their own construction.

Determining the occurrence of predation versus web-stealing may help clarify the importance of self prey capture (capturing its own insect prey) for *A. trigonum*. Once an *A. trigonum* had usurped a host’s web, most emigrated from that web after 1–2 days. Because a web devoid of its host can last about 3–6 days, it appears that predation is usually the goal (whether or not the *A. trigonum* was successful). Nonetheless, 29% of *A. trigonum* in unoccupied *N. radiata* webs, and 24% of *A. trigonum* in unoccupied *P. costatus* webs, stayed for three days or longer with one individual remaining in the same *N. radiata* web for 45 days. Additionally, since empty webs that are invaded by *A. trigonum* last longer than those that are not, this implies that either *A. trigonum* is expending energy in maintenance and repair of the web, or staying in

those webs that happen to last longer. The individual that resided in the same web for 45 days definitely added silk and altered the web considerably so that it was no longer recognizable as a *N. radiata* web. One might view this as stealing the web site rather than just the web. In any case, using the host web for prey capture seems to be an important foraging mode for a substantial portion of the population. (One note of caution with this conclusion relates to the fact that the *A. trigonum* emigration frequency distribution in Fig. 6 follows an exponential decay function. Suter & Sanchez (1991) have presented strong evidence that such relationships may indicate a "rolling dice" criterion for decision making, especially if those organisms face an unpredictable environment. If this is true here, some individuals may just be randomly waiting longer before moving on to their next predation attempt). *Argyroides* almost certainly evolved from web-building ancestors, and their current use of self prey capture may still represent a significant amount of their food intake for some species and therefore be more than just a evolutionary vestige.

Whitehouse's (1986) proposed models for the evolution of kleptoparasitism in *Argyroides* imply that although both araneophagy and kleptoparasitism are present in most species, the foraging behavior of all ancestors and current species of *Argyroides* is dominated by a single strategy. But these data show that there appears to be no consistent dominant foraging mode for *A. trigonum*, and which strategy it uses depends largely upon the abundance and species of hosts (or prey spiders) that are available. Other environmental factors such as insect availability probably influence *A. trigonum* foraging mode as well and should be investigated in the future.

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## **BIONOMICS OF THE SPIDER, *CROSSOPRIZA LYONI* (ARANEAE, PHOLCIDAE), A PREDATOR OF DENGUE VECTORS IN THAILAND**

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**ABSTRACT.** The pholcid spider, *Crossopriza lyoni* (Blackwall 1867) is a common inhabitant of homes in a rural village in Chachoengsao Province, Thailand. Studies on the spider were initiated because its microhabitat closely coincided with that of adult *Aedes aegypti* (Linnaeus 1762), mosquito vectors of dengue virus. Laboratory observations showed that females deposited eggs 4–6 days after copulation. Females held the egg sac in their mouthparts for 11–13 days, until all spiderlings (mean = 34) had left the sac. Spiderlings did not feed until they had molted, but as soon as feeding commenced they were capable of overpowering a mosquito many times their own size. Sometimes spiderlings would share a single mosquito or eat a mosquito wrapped by the mother spider. Spiderlings separated from their mother grew more rapidly than those left with the mother and reached maturity in as little as 74 days. The spiders' principal means of capturing prey was to throw silk with the aid of the hind legs. Spiders used this method to immobilize mosquitoes which were entangled in the standing web or to catch flying mosquitoes. The mosquito was not bitten until the time of feeding, up to six days after capture. Feeding occurred on only 34–48% of the days, and spiders ate about one mosquito per day. Cannibalism was a significant mortality factor, accounting for 67–84% mortality in a cage of spiderlings. An enzyme-linked immunosorbent assay (ELISA) was adapted to test spider tissue for presence of dengue virus. The ELISA was used to show that spiders did not become infected when fed dengue-infected mosquitoes. The results of the study suggested that *C. lyoni* could form an important component of integrated control of *Aedes aegypti* mosquitoes in foci of dengue transmission.

Mosquitoes have a tremendous impact on humans almost everywhere, either as significant sources of irritation or as vectors of serious disease. Dengue is the most common viral pathogen transmitted by mosquitoes. The virus, which consists of four distinct serotypes, causes a spectrum of disease ranging from mild fever to fatal shock. Since the late 1970's, occurrence of the disease has steadily expanded throughout the tropics and subtropics, to the point that there are millions of cases every year. All confirmed vectors of dengue virus are in the genus *Aedes* and the most im-

portant vector is *Ae. aegypti* (Linnaeus 1762) (Gubler 1988). This mosquito thrives in association with humans, larvae of the species developing in almost any water-filled container (Christophers 1960). In at least some geographical areas, the adult females of *Ae. aegypti* preferentially bite humans indoors (Scott et al. 1993).

Spiders can be efficient predators of adult mosquitoes both outdoors and indoors. Studies on spider predation of mosquitoes have examined whether various spider species eat mosquitoes. For example, detailed observations on the rate at which spiders ate mosquitoes located in large cages in a Polish forest indicated that species of spiders varied in their

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appetite for mosquitoes and that the rate of consumption was not constant over time (Dabrowska-Prot et al. 1966, 1968). Other observations have shown that spiders eat mosquitoes in Japanese homes (Ori 1974) and in the prairies of Nebraska (Rapp 1978). Another approach has been to test wild-caught spiders for the presence of mosquito antigen in their guts by the use of antibody-based tests. This method showed that a large proportion of spiders in Kenyan homes were eating mosquito vectors of malaria (Service 1973). In Malaysia, spiders were eating *Ae. albopictus* (Skuse 1894), mosquito vectors of dengue outdoors (Sulaiman et al. 1990a), and *Ae. aegypti* vectors indoors (Sulaiman et al. 1990b). We saw only one study in which an attempt was made to determine whether spiders had a significant impact on a mosquito population in the field (Ramoska & Sweet 1981). That study found that discarded tires colonized by spiders contained fewer mosquito larvae than those tires without spiders. Since spiders generally eat a variety of prey, their usefulness as a biocontrol agent of mosquitoes would depend on the relative abundance of mosquitoes and other prey species. Maximum effect from spiders could be expected where the microhabitat of the mosquito and the spider coincide so that a large proportion of prey are mosquitoes.

While studying dengue virus transmission in rural Thailand, we noticed populations of *Crossopriza lyoni* (Blackwall 1867) (Araneae, Pholcidae) in village homes. The spiders were commonly seen in their webs, constructed under homes and in undisturbed areas of the primitively constructed walls. *Crossopriza lyoni* generally inhabit the interiors of buildings and other protected areas in southern Asia and Japan. Most of the literature on the species is restricted to taxonomic treatments (Yaginuma 1986; Kim 1988; Koh 1989) and studies on limited aspects of its physiology and behavior (Maya et al. 1982; Karuppswamy et al. 1984; Downes 1987). One Indian study (Nandi & Raut 1985) noted that *C. lyoni* eats *Aedes* species indoors.

We suspected that the spiders could have an influence on adult populations of the dengue vector because the microhabitat of the spiders corresponded closely to the distribution of adult *Ae. aegypti* indoors. Predation on adult mosquitoes might be particularly significant in reducing transmission of dengue by *Ae. ae-*

*gypti*, since the adult population includes older females which have survived long enough to acquire the virus and incubate it to infectious levels. In order to evaluate the possible role of *C. lyoni* in the ecology of dengue transmission, we made observations on bionomics of reproduction, development, and mosquito predation of the spider. In addition, we performed experiments to determine whether the spider might harbor dengue virus following feeding on an infected mosquito.

## METHODS

**Spiders.**—Spiders were collected in and around homes of a village (official designation was Village 6) located 100 km east of Bangkok in Hua Sam Rong District, Plaeng Yao County, Chachoengsao Province, Thailand. The spiders were captured incidentally during weekly sampling for *Aedes aegypti* (Edman et al. 1992; Scott et al. 1993). Not all spiders were retained and no attempt was made to quantify the abundance or variety of spider species. The spiders used in this study were perceived to be the most abundant kind during initial sampling.

The pholcid specimens were identified as *Crossopriza lyoni* from the habitus, presence of depressed thoracic fovea, eye pattern, distinct abdominal shape, morphology of the male left palpus, and morphology of the dissected and cleared female epigynum (Yaginuma 1986; Kim 1986; Koh 1989). Voucher specimens of *C. lyoni* are deposited in the U.S. National Museum arachnid collection. The authors are confident of the identifications, since the third author has taxonomic experience with spiders and the specimens were carefully examined. It is possible that houses in the field also contained separate but morphologically similar species, because we did not perform a thorough survey of all spiders in the area. The work reported in this paper, however, was certainly performed on the stated species, since specimens were examined from representative familial lines reared in the laboratory.

The device for sampling was a commercial vacuum cleaner fitted with a screen-backed collection carton (12 cm diameter) affixed to a 0.5 m long section of PVC pipe. The pipe with the carton at the end was applied to crevices and spaces on the interior and exterior sides of the walls of the houses. Samples were

quickly chilled over wet ice and then refrigerated at 4 °C overnight before sorting.

Spiders were maintained in the laboratory at 30 °C (a representative temperature of the interior of village homes) and equal photophase and scotophase of 15 h. The spiders were kept in clear plastic cages (13 × 8 × 6.5 cm high) with tight lids. The lids were fitted with a small hole to introduce food and a 2-cm hole covered with screen for ventilation. The screen was covered with a square of gauze, which was wetted daily.

**Behavioral and developmental observations.**—Observations on behavior, feeding, and development were made during nine months on 13 different cages of spiders collected January–March 1991. In addition to general observations, quantitative measurements were made on growth of spiderlings and on rate of feeding by adult female spiders.

Growth was observed by measurements of body length (chelicerae to posterior of abdomen) twice per week, accomplished with the aid of a drawing tube attached to a dissecting microscope. The drawing tube was positioned over a digitizing tablet (Numonics Corp., Montgomeryville, Pennsylvania) and the length recorded by placing the pointing device of the tablet over the perceived image of a spiderling. Sigma Scan software (Jandel Scientific, Inc., Corte Madera, California) was used to calibrate the tablet and to record and analyze the data. Spiderlings were from a single egg sac, but were divided one day after hatching into a group of 25 in a cage by themselves, and 24 in a cage with their mother. Data were analyzed with an independent *t*-test, comparing the difference between the mean lengths of spiderlings in the two cages each day that measurements were made. Throughout the 71 days of measurements, cages had constant access to an excess of *Anopheles dirus* Peyton and Harrison 1979 mosquitoes for food.

The number of mosquitoes eaten by female spiders was recorded for three individuals fed *An. dirus* and for two individuals fed *Ae. aegypti*. Each day, the number of mosquitoes consumed by a spider was recorded and an excess of mosquitoes added to each cage. If all mosquitoes were consumed, a greater number of mosquitoes was added the next day.

**Dengue virus experiment.**—An experi-

ment was performed to determine whether dengue virus in mosquitoes eaten by spiders could subsequently infect the spiders. Male *Ae. aegypti* mosquitoes were injected in the thorax with 0.017 µl of a tissue culture suspension of dengue 2 virus (10<sup>6</sup> plaque-forming units (PFU)/ml) and then held at 32 °C for 10 days to allow time for the virus to amplify. In our laboratory, this procedure had been found to infect in excess of 90% of mosquitoes. Live infected mosquitoes (uninfected mosquitoes for controls) were fed to individually caged spiders which had been reared to maturity in the laboratory from eggs deposited by field-caught females. All spiders ate either three or four infected mosquitoes. After either 14 or 28 days, the spiders (one control and five virus-fed spiders for each time interval) were dissected into three pieces which were subsequently kept cold over wet ice. The pieces were: 1) poison gland, prepared by cutting a wedge from between the first and second legs on each side to the area just behind the eyes, 2) prosoma, prepared from the remainder of the prosoma, and 3) abdomen. For the 14-day samples, the poison gland was triturated in 150 µl, and the prosoma and abdomen each in 300 µl of 20% fetal bovine serum in phosphate buffered saline (FCS-PBS). For the 28-day sample, all parts were triturated in 500 µl of FCS-PBS. Each triturate was injected into five *Toxorhynchites splendens* (Wiedemann 1819) mosquitoes for amplification and detection of dengue virus (Rosen 1981). The number of poison gland triturates was limited to two virus-fed and one control spider for each time interval. The *Tx. splendens* mosquitoes were held for 12 days at 30 °C before examining them for signs of infection using indirect immunofluorescent assay of head squashes (Sithiprasasna et al. 1994). In addition, aliquots of the triturates were frozen at –70 °C until being tested using a double sandwich enzyme-linked immunosorbent assay (ELISA) designed to detect dengue virus (Sithiprasasna et al. 1994). Controls were run with the ELISA to determine the sensitivity of the method used on spider tissue, triturating each tissue in 800 µl of FCS-PBS. Five replicates of each control preparation were run, consisting of serial dilutions of dengue 2 seed (10<sup>6</sup> PFU/ml) diluted in either FCS-PBS, previously-frozen spider triturates, or fresh spider triturates.



### RESULTS

Most spiders were collected from the interiors of homes between exposed support beams or behind furniture. Some spiders were also collected in the 1–3 m space under houses with elevated floors. The homes had wooden floors, either wooden or bamboo walls, and metal or cement composite roofs. Construction left many gaps in the walls and floors, forming holes that opened directly outdoors. *Aedes aegypti* mosquitoes were abundant indoors (Edman et al. 1992; Scott et al. 1993) because of the open nature of the houses and because of the storage of large amounts of water for household use.

Spiders copulated readily in the laboratory. In one case, a single male (70 days old, reared in the laboratory) copulated successfully with three females during a nine day period. The first time was observed immediately after the male was introduced into the cage of a female collected in the field 50 days before. The pair remained in copula for 40 minutes, with the female oriented ventral side up and the male facing her posterior with both palpi inserted into her genital orifice. The male was exposed to two other females for one day each, one collected 94 days and the other 116 days previously. The third female ate the male, but apparently had copulated successfully. Fertile eggs were deposited 6, 4, and 5 days after copulation with each female, respectively.

Oviposition was not observed directly, but resulted in an egg sac held in the mouthparts of the female, as is typical of the family. Cottony flecks in the web were observed 10 times in association with oviposition (occurring up to four days before and five days after) and six times not in association with oviposition. On one occasion, six eggs fell from an egg sac to the floor of the cage and subsequently did not hatch. The number of spiderlings hatching from 12 sacs deposited by nine spiders ranged from 5–54 with a mean of 34 ( $\pm$ SD = 14.8) spiderlings. Eggs failed to hatch only once. In most instances, hatching was noted when spiderlings were seen in the mother's web, 11–13 days after oviposition. In one case, closer observation indicated that the spiderlings partially emerged from their eggs three days before they actually left the egg sac. The mother would hold onto the egg sac

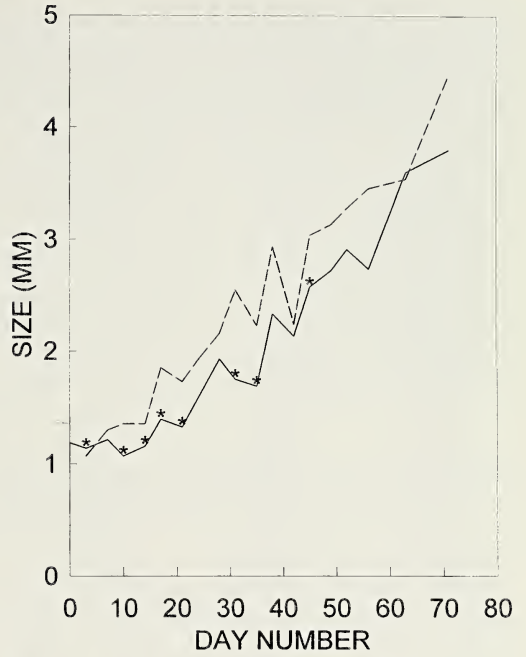


Figure 1.—Length of *Crossoprizia lyoni* spiderlings emerging on Day 0 from a single egg sac, fed an excess of *Anopheles dirus* mosquitoes, and measured twice weekly. Twenty-four spiderlings remained in the cage with their mother (solid line) and 25 spiderlings were placed in a cage by themselves (dashed line). Asterisks indicate days on which there was a statistically significant ( $P \leq 0.05$ ) difference in length.

until all spiderlings had left it, even when this process took more than one day.

Spiderlings were inactive for the first 2–4 (mode = 3) days after leaving the egg sac, when molting occurred. Growth continued during the entire 71 days that spiderlings were measured (Fig. 1). Those spiderlings that had been left with their mother were consistently smaller than those spiderlings in a cage without an adult spider. This size difference was observed until the end of the measurement period, at which time there was no significant difference in size. The spiderlings separated from the mother matured more rapidly and deposited their first egg sac when 74 days old, compared to 80 days for those spiders left with their mother. Mature females had a mean weight of 28.6 mg ( $n = 15$ , SD = 7.79, range: 18.2–44.6), 63% greater than the mean weight for males (17.6 mg,  $n = 9$ , SD = 3.73, range: 11.8–23.4). Although we did not hold laboratory-reared spiders long enough to get an

Table 1.—Number of mosquitoes (*Anopheles dirus* or *Aedes aegypti*) eaten by mature, female, individually-caged *Crossopriza lyoni*. Replicate spider #1 had male present 7 days; spider #4 had male present 11 days. Prey species “d” was *An. dirus*, prey species “a” was *Ae. aegypti*.

	Replicate spider					Mean
	1	2	3	4	5	
Prey species	d	d	d	a	a	
No. of days	67	67	67	66	66	
Spider weight (mg)	37	45	23	42	25	34.4
Mean eaten per day	1.6	0.81	1.4	0.89	0.73	1.1
SD eaten per day	1.3	0.87	1.4	1.1	0.85	1.2
Max. eaten per day	4	4	6	4	3	4.2
% days not eating	40	42	34	47	48	42.2

accurate estimate of longevity, we observed that wild-caught mature females lived as long as 120 days in the laboratory, implying longevity of at least 194 days.

Mature spiders captured mosquitoes which landed on their webs or which flew nearby. Hungry spiders actively pursued prey within their cages, generally capturing the mosquito within seconds of its introduction. The spider threw silk over the mosquito, the spider guiding the silk with its hind legs. The prey was then wrapped loosely in silk by manipulating the silk with abdomen and hind legs, but without rotating the prey. The first time a spider bit its prey was at the time of consumption, sometimes delayed as long as six days after capture. The quantity of mosquitoes consumed (Table 1) varied among individual spiders, but generally approached one mosquito per day, regardless of mosquito species. Feeding was discontinuous, with spiders fasting 34–48% of the days. Spiders with egg sacs continued to feed at approximately the same rate, setting aside the egg sac temporarily in order to consume the prey. Feces appeared as dark, tarry spots on the floor of the cage.

Spiderlings began feeding 2–4 days after their first molt, at which time they could overpower a mosquito which was 4.0 mm long (i.e., approximately 4× the length of the spider). Up to three spiderlings at once sometimes fed on a single, wrapped mosquito. Spiderlings sometimes fed on a mosquito wrapped by their mother or caught in their mother’s web. Three different cohorts of spiderlings ate between 0.178–0.523 mosquitoes per spiderling per day during the first 11–17 days after beginning to eat. Cannibalism was common among the spiderlings, especially

following introduction of mosquitoes when activity was at its greatest. Although probably an artifact of the confined conditions within a cage, cannibalism caused 67–84% mortality in four separate cohorts which were maintained until maturity.

*Toxorhynchites splendens* were not infected by triturates from spiders which had fed on dengue-infected mosquitoes. Also, none of the spider triturates were positive for virus in the ELISA. The ELISA was sufficiently sensitive to detect a dilution of 1:160 ( $6.25 \times 10^3$  PFU/ml) of the virus seed in any of the fresh or frozen spider tissue triturates (Table 2).

DISCUSSION

Our laboratory observations on *C. lyoni* help fill in some of the gaps in bionomic knowledge of this species. Females deposited eggs shortly after copulation. The male was capable of mating successfully at least three times over a nine-day period, suggesting that a small number of males could keep a large group of females inseminated. Despite previous reports (Downs 1987), we saw no evidence of the female eating any of her own eggs, possibly because most eggs were fertile. Prey-capturing techniques were described in detail by Nandi & Raut (1985), including manipulation of silk and prey with the hind legs and biting only at the time of feeding. In addition, they noted that the spiders actively removed carcasses of prey from the web.

One of the interesting aspects of the spiders’ behavior was the interaction of the spiderlings with their mother and with each other. The mother spider could evidently sense the presence of spiderlings in the egg sac, since the sac was retained until all spiderlings had



Table 2.—ELISA sensitivity to dengue 2 virus (seed from tissue culture, 10<sup>6</sup> PFU/ml) in *Crossopriz* *lyoni* tissue triturates.

Diluent source	Virus dilution	n	Mean optical density (O.D.)		
			Poison gland	Prosoma	Abdomen
Virus seed	1:2	5	0.550	0.347	0.447
	1:8	5	0.301	0.193	0.298
	1:16	5	0.224	0.164	0.207
	1:32	5	0.179	0.128	0.154
Fresh spider	1:5	5	0.305	0.287	0.313
	1:40	5	0.126	0.106	0.091
	1:80	5	0.093	0.088	0.080
	1:160	5	0.099	0.079	0.066
Frozen spider	1:5	5	0.291	0.350	0.312
	1:40	5	0.115	0.108	0.096
	1:80	5	0.098	0.087	0.079
	1:160	5	0.080	0.082	0.068
Cutoff value		2	0.080	0.052	0.058
Infected <i>Toxorhynchites</i>			0.182	0.164	0.186

left it. The mother's hunting activity sometimes benefitted the spiderlings when they ate mosquitoes captured and wrapped by their mother or mosquitoes trapped in the mother's web. Despite the apparent advantages near their mother, spiderlings kept by themselves grew and matured significantly faster than those kept with their mother, probably because they conserved energy which would have been spent following disturbance by the mother and because they were not competing with the mother for food. Among themselves, the spiderlings interacted in at least two ways. First, several spiderlings sometimes fed simultaneously on the same mosquito. Second, the spiderlings ate each other, especially when excited by the introduction of prey. Such cannibalism was a significant mortality factor in the confined conditions of a cage, though it was not observed in the field.

We thought there was a possibility that spiders could harbor dengue virus, since spiders in village homes undoubtedly eat infected *Ae. aegypti*. Our laboratory experiment failed to demonstrate the presence of virus in spiders which had fed on dengue-infected mosquitoes. Triturates of the spiders were negative for virus when injected into *Toxorhynchites* and when triturates were tested directly with an ELISA capable of detecting low titers of virus in spider tissues.

Judging from observations of spiders feed-

ing on mosquitoes in the laboratory, spiders could have a significant impact on the population of *Ae. aegypti* in a home. Our estimate of consumption was about one mosquito per mature female spider per day, but under other conditions this rate might be much higher. By feeding recently killed mosquitoes to *C. lyoni* occurring naturally in a house, Nandi & Raut (1985) observed that a single spider ate 12–20 mosquitoes per day for 2–3 consecutive days. Although we did not survey for other prey, small flies and spiders could have formed a part of the diet of *C. lyoni* in the field, diluting its effect on mosquitoes. It is significant, however, that juvenile and mature spiders were efficient at capturing mosquitoes and frequented the dark corners and walls of homes, corresponding to the locations favored by *Ae. aegypti* (Sheppard et al. 1969; Kusakabe & Ikeshoji 1990). Although we did not determine the number of spiders in village homes, all available microhabitats were usually occupied. The potential significance of this predator raises the possibility that insecticidal application directed at *Ae. aegypti* adults indoors might actually exacerbate the dengue problem in rural Thailand. Indoor insecticidal fogging might eliminate both mosquitoes and spiders from inside a home, but the mosquitoes could quickly recolonize the house from existing larval sources. On the other hand, the spider population would re-

cover much more slowly because a greater proportion of the total population would have been exposed to insecticide and the spider's reproductive rate is far lower than that of the mosquito (Christophers 1960).

*Crossopriza lyoni* could prove valuable as an intentionally managed biocontrol agent for reduction of *Ae. aegypti* populations and dengue transmission. There is precedence for the use of spiders to control a public health pest indoors, an example being the successful reduction of fly populations and subsequent transmission of gastrointestinal pathogens (Nyffeler & Benz 1987). Introduction of *C. lyoni* into homes without spiders could result in a constant population, self-regulated by cannibalism and availability of appropriate microhabitats. Because spiders eat a variety of prey, they would tend to maintain their presence even when mosquitoes were scarce. As a result, spiders would be present to blunt sudden mosquito population outbreaks (Riechert 1974). Such outbreaks can occur when rains fill many containers at once, hatching mosquito eggs in all of them simultaneously. Where the spiders occur naturally, efforts could be made to avoid killing spiders during housecleaning or insecticidal application. The presence of dengue where the spiders now occur shows that spiders alone do not stop transmission; however, management of spider populations might provide the additional control of adult mosquitoes needed to block dengue transmission following reduction of larval populations by other, non-insecticidal means (e.g., Kittayapong & Strickman 1993).

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## LEG AUTOTOMY AND AVOIDANCE BEHAVIOR IN RESPONSE TO A PREDATOR IN THE WOLF SPIDER, *SCHIZOCOSA AVIDA* (ARANEAE, LYCOSIDAE)

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**ABSTRACT.** The wolf spider, *Schizocosa avida* (Walckenaer 1838) can utilize leg autotomy to successfully avoid capture by the scorpion, *Centruroides vittatus* (Say 1821). Leg autotomy was used successfully in 7 out of 43 encounters with a scorpion (16%). Spiders were captured and eaten by scorpions in 79% of the encounters. Two spiders (5%) escaped capture by means other than leg autotomy. Scorpions most often grasped spiders at their abdomen (49%), followed by the cephalothorax (35%) and leg (16%). Naive spiders (no previous experience with a scorpion), with intact legs or an autotomized leg, spent significantly more time (26–32 min out of a 60-min trial) on a filter paper disc that had come into previous contact with a scorpion as compared to spiders that had lost a leg in a successful escape from an encounter with the predator (10 min). This is an example of associative avoidance learning and is the first demonstration of this type of learning in response to previous experience with a predator in spiders.

The autotomy of various bodily structures in response to attack by predators has been reported for many species (Robinson et al. 1970; Edmunds 1974). Tail autotomy has been shown to enhance survival in salamanders (Brodie 1983) and lizards (Punzo 1982; Arnold 1988). Decapod crustaceans (Spiviak & Politis 1989) and spiders (Foelix 1982; Formanowicz 1990) frequently autotomize their legs when grasped by predators.

In the present study, I analyzed the effectiveness of leg autotomy as an antipredator strategy in the wolf spider, *Schizocosa avida* (Walckenaer 1838), against a naturally occurring scorpion predator, *Centruroides vittatus* (family Buthidae). I also investigated the effects of previous encounters with the predator on the avoidance behavior of *S. avida*.

### METHODS

I collected adult females of *S. avida* in Brewster County, Texas, during May–July 1994. Spiders carrying egg sacs were located at night using a headlamp. Scorpions (*C. vittatus*) from the same area were located using a portable UV light (BioQuip Model 2813C, Gardena, California). Animals were placed individually in plastic holding containers and transported to the laboratory for subsequent studies. Voucher specimens of *S. avida* and *C. vittatus* have been deposited in the University of Tampa Invertebrate Collection.

All experiments were conducted on adult female spiders (body length: 11–14 mm) reared from egg cases collected in the field. Spiderlings emerging from egg cases were reared in an environmental chamber (Percival Model I-37, Boone, Iowa) maintained at 20 °C, 68–72% relative humidity (RH), and a 12L:12D photoperiod regime. Spiderlings were housed individually in plastic containers and fed on a mixed diet of flies (*Drosophila melanogaster* and *D. virilis*) and cockroach (*Periplaneta americana*) nymphs. Water was provided *ad libitum*. As the spiders grew in size, larger prey were used (adult crickets, cockroaches and beetles). As a result of these rearing procedures, all spiders were naive in the sense that they had no prior experience with the scorpion, *Centruroides vittatus*, which is sympatric with *Schizocosa avida* in Brewster County, Texas. Adult female scorpions (0.419 g  $\pm$  0.21) were maintained under the same conditions and fed on a diet of crickets, grasshoppers and a variety of spiders collected locally in Hillsborough County, Florida. Scorpions were deprived of food for 72 h prior to any encounter with a spider.

**Encounter experiments.**—Each encounter between a scorpion and a spider was conducted in a clear acrylic plastic (Plexiglass™) chamber (15  $\times$  10  $\times$  10 cm) at room temperature. The chamber was situated on a wooden



table behind a one-way mirror to minimize disturbance to the animals during encounter sequences. The floor of the chamber contained 3 cm of sand as a substrate. All spiders used in these experiments were fed 24 h prior to an encounter with a predator, and possessed all of their legs. A scorpion was placed in the chamber for 24 h prior to an encounter with a spider. I staged a total of 50 encounters (trials) between different spiders and scorpions. Each spider and scorpion was tested only once. At the start of each trial, a spider was placed at the center of the encounter chamber which contained one randomly chosen scorpion. I carefully observed both animals and verbally recorded their activities using a Sony HP-110 tape recorder. In seven of the trials, the scorpions made no attempt to capture the spider. Only those data obtained from trials in which a scorpion attempted to capture a spider ( $n = 43$ ) were used for statistical analysis. A trial ended when the spider was either successfully captured and ingested by a scorpion, escaped an initial strike without utilizing leg autotomy, or escaped via leg autotomy. Data were analyzed using the  $G$ -test of independence as described by Sokal & Rohlf (1981). All encounters were recorded on a Panasonic L3 video recorder for subsequent study as previously described by Punzo (1995).

**Effect of previous encounter.**—In a second set of experiments using different spiders and scorpions, I tested the effects of a previous encounter with *C. vittatus* on the subsequent behavior of three groups of *S. avida*. One group of spiders (G1,  $n = 15$ ) consisted of individuals who had all of their legs intact and had never encountered a scorpion throughout their lives. Another group (G2) consisted of 15 different spiders who had also never encountered a scorpion; in this group, however, one of their legs (chosen at random) was autotomized after being grasped by a pair of forceps. The third group (G3) consisted of 15 spiders who had one previous experience with a scorpion and had used leg autotomy to successfully escape capture by the predator. In these experiments, a spider was placed randomly into either end of a glass chamber (15 × 15 × 8 cm) containing two, square-shaped pieces of filter paper (Whatman No. 1) situated side-by-side and covering the entire floor of the chamber. One of the pieces of filter paper was taken from the floor of a plastic con-

tainer housing a scorpion (treated), allowing *C. vittatus* to come into contact repeatedly with the filter paper during the course of its normal activities (for a period of two days). The other fresh piece of filter paper (untreated) had not been in contact with a scorpion. For each trial, the positions of the two pieces of filter paper (to the right or left) on the floor of the chamber was determined using a table of random numbers. The length of each trial was 60 min, and the amount of time (in min) spent by each spider on both pieces of filter paper was recorded with a stopwatch. A Duncan multiple range test (Sokal & Rohlf 1981) was used to analyze the data.

## RESULTS

In encounters with scorpions, *S. avida* females were successfully captured and eaten in 79% of the trials (34 out of 43 trials). Nine spiders escaped capture; seven of these (78%) utilized leg autotomy. During prey capture, scorpions grasped the spider using one of their pedipalps. Spiders were either grasped by their abdomen (49%), cephalothorax (35%) or leg (16%). Only two of the nine spiders (22%) escaped capture without utilizing leg autotomy. These two spiders were grasped at the distal end of the abdomen and lateral region of the cephalothorax and escaped by pulling free from the pedipalps. Sixteen percent of the spiders were grasped by a leg and escaped after autotomizing the limb. Significantly more spiders escaped capture by utilizing leg autotomy than those who escaped by struggling free ( $G = 34.9$ ,  $df = 1$ ,  $P < 0.001$ ). Scorpions were observed feeding on the autotomized leg while the spider ran to the other end of the chamber.

The effects of previous encounters with a predator on the subsequent behavior of *S. avida* are shown in Figure 1. There was no significant difference in the mean amount of time spent on a treated (contact with scorpion) versus untreated (no contact with scorpion) pieces of filter paper between G1 (legs intact, no previous encounter with predator) and G2 (leg autotomized, no previous experience) spiders ( $P > 0.50$ ). However, spiders that had previously escaped by autotomizing a leg (G3) spent significantly less time on treated filter paper (10 min out of a 60 min trial) as compared to untreated filter paper (50 min) ( $P < 0.001$ ).

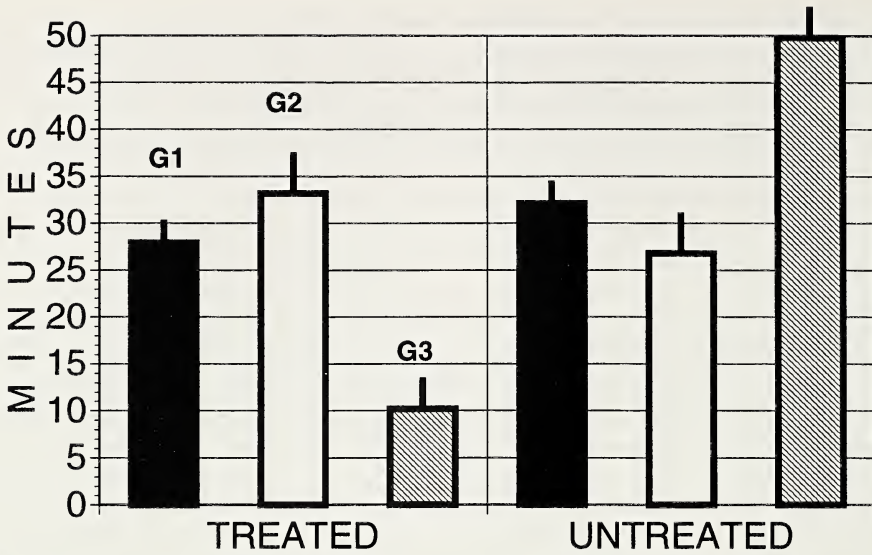


Figure 1.—The effects of previous encounter experience with the scorpion *Centruroides vittatus* on the behavior of three groups (G1, G2, G3) of *Schizocosa avida*. Values represent the mean amount of time (in minutes) that *Schizocosa avida* females remained on square pieces of filter paper that had been exposed to the presence of *Centruroides vittatus* (treated) as compared to discs that had not been contacted by the scorpion (untreated). G1 = spiders with legs intact, no previous experience with a scorpion; G2 = leg autotomized, no previous experience with a scorpion; G3 = leg autotomized in an encounter with a scorpion. Vertical lines represent SD. See text for details.

### DISCUSSION

This study demonstrates that *S. avida* can utilize leg autotomy to escape capture by a natural predator if grasped by the leg. A previous study by Formanowicz (1990) showed that a filistatid spider, *Kukulcania hibernalis* (Chamberlin 1926) from Wise County, Texas, was also able to utilize leg autotomy to escape predation by *C.entruiroides vittatus*. However, this strategy was not an effective defense against a centipede predator (*Scolopendra polymorpha*). In the present study, leg autotomy resulted in a successful escape in 16% of the encounters for the wolf spider *S. avida*, whereas *K. hibernalis* successfully utilized this strategy in 36% of its encounters with a scorpion.

The site of autotomy was always at the junction (intersegmental membrane) between the coxa and trochanter of the leg grasped by the scorpion. This is in agreement with the previous literature on leg autotomy in spiders (Robinson et al. 1970; Foelix 1982) and some insects (Pearson 1985). In all cases, once the spider was grasped by a scorpion, it exhibited a rapid upward movement of the coxa. The

rest of the distal portion of the leg remained in a relatively fixed in position.

This study also shows that once *S. avida* has had an encounter experience with *C. vittatus* and is successful in escaping capture, it will avoid a substrate that has been previously occupied by this scorpion. This suggests that the spider can remember some cue (probably olfactory in nature) associated with the scorpion and use that information to avoid the predator at a later time. This is an example of rapid associative avoidance learning (Punzo 1985, 1996) and represents the first demonstration that a spider can utilize this type of behavioral plasticity to avoid predators. Although this spider and scorpion have presumably coexisted sympatrically for a long period of time, there is no indication that *S. avida* possesses an innate capacity to recognize the presence of this predator. Spiders that had no previous encounter experience with the scorpion did not demonstrate avoidance of a substrate previously occupied by *C. vittatus*.

### ACKNOWLEDGMENTS

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## **TUBEROCHERNES (PSEUDOSCORPIONIDA, CHERNETIDAE), A NEW GENUS WITH SPECIES IN CAVES IN CALIFORNIA AND ARIZONA**

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**ABSTRACT.** A new genus, *Tuberochernes*, is defined, the type species being *T. aalbui* new species, from a cave in Mono County, California. Another species referable to the genus is described also, *T. ubicki* new species, from a cave in Santa Cruz County, Arizona. Unique modifications of the palpal chelae and first legs of the males are discussed.

Among some pseudoscorpions collected in caves in California and Arizona by Rolf Aalbu, Derham Giuliani, and Darrell Ubick were some specimens with striking modifications of the palpal chelae and first legs of males. The combination of these features, unique among pseudoscorpions, warrants the description of two new species and the establishment of a new genus.

### **METHODS**

Animals were collected in pitfall traps containing ethylene glycol or directly into alcohol, and were stored in alcohol. Specimens were prepared for detailed study by dissection, clearing in clove oil, and mounting in Canada balsam on microscope slides, generally following the procedure described by Hoff (1949). They were studied and measured under a compound microscope, and drawings were made by direct projection of the image onto paper. The specimens are deposited, as indicated, in the California Academy of Sciences, San Francisco, California (CAS) and the Florida State Collection of Arthropods, Gainesville, Florida (FSCA).

A few abbreviations are used in the text: L = length; L/B = ratio, length/breadth; L/D = ratio, length/depth; T = tactile seta.

### **Family Chernetidae Menge**

Chernetidae Menge 1855:22; Muchmore 1982:101;  
Harvey 1991:534 (complete synonymy to 1988);  
Harvey 1992:1427.

### ***Tuberochernes* new genus**

**Type species.**—*Tuberochernes aalbui* Muchmore new species.

**Diagnosis.**—*Tuberochernes* is unique among known chernetid pseudoscorpions in the possession of the following suite of characters: 1) cheliceral flagellum of four setae; 2) spermathecae of female consist of two long tubes with terminal sacs; 3) male (but not female) with a conspicuous conical protuberance on the medial side of the hand of the palpal chela; 4) tarsus of leg I of male (but not female) distinctively shortened and curved; 5) tarsus of leg IV (both sexes) with a short, distally located, tactile seta, variably acuminate or finely denticulate. It appears most closely related to *Mirochernes* Beier 1930, from which it can be distinguished readily by the much larger and more complex process on the chelal hand of the latter.

**Description.**—A genus of the family Chernetidae. Palps well sclerotized, reddish-brown, carapace light brown, other parts lighter. Surfaces of carapace and palps heavily granulate, with slender clavodentate setae. Carapace with two distinct, transverse furrows; without eyes; with 70–100 setae, four at anterior and 12–20 at posterior margin. Most tergites and sternites divided; middle tergites with 25–30 and sternites with about 20 setae. Cheliceral hand usually with six setae (occasionally five), *bs*, *sbs* and *xs* denticulate, *es* short and either acuminate or finely denticulate; flagellum of four setae, the two distal ones long, serrate, the two proximal ones short, simple; galea slender, with 4–6 small rami. Palp rather slender, sexually dimorphic; trochanter, femur and patella of both sexes, and chela of female, typically chernetid in proportions; chela of male heavi-



er than that of female, with a large, broad-based, conical protuberance on medial side of hand, and with movable finger distinctly bowed. Chelal fingers with 45–50 cusped marginal teeth, and with many external and a few internal accessory teeth. Venom apparatus developed only in movable finger. Trichobothria as shown in Fig. 4; on fixed finger, *ist* well distad of *est*, and *ib* distad of *esb*; on movable finger, *st* distinctly closer to *t* than to *sb*. Leg I sexually dimorphic, especially in *T. ubicki* new species; segments more robust in male than in female; tarsus of male curved, while that of female straight. Leg IV quite slender. Tarsus IV with a short, distally located, tactile seta; this seta is sometimes acuminate, sometimes denticulate at tip. Male genitalia typically chernetid in form; spermathecae of female are thin tubes with irregular, ovoid end sacs.

Two species are presently assigned to *Tuberochernes*, namely *T. aalbei* new species from Mono County California, and *T. ubicki* new species from Santa Cruz County, Arizona, as described below.

***Tuberochernes aalbei* new species**

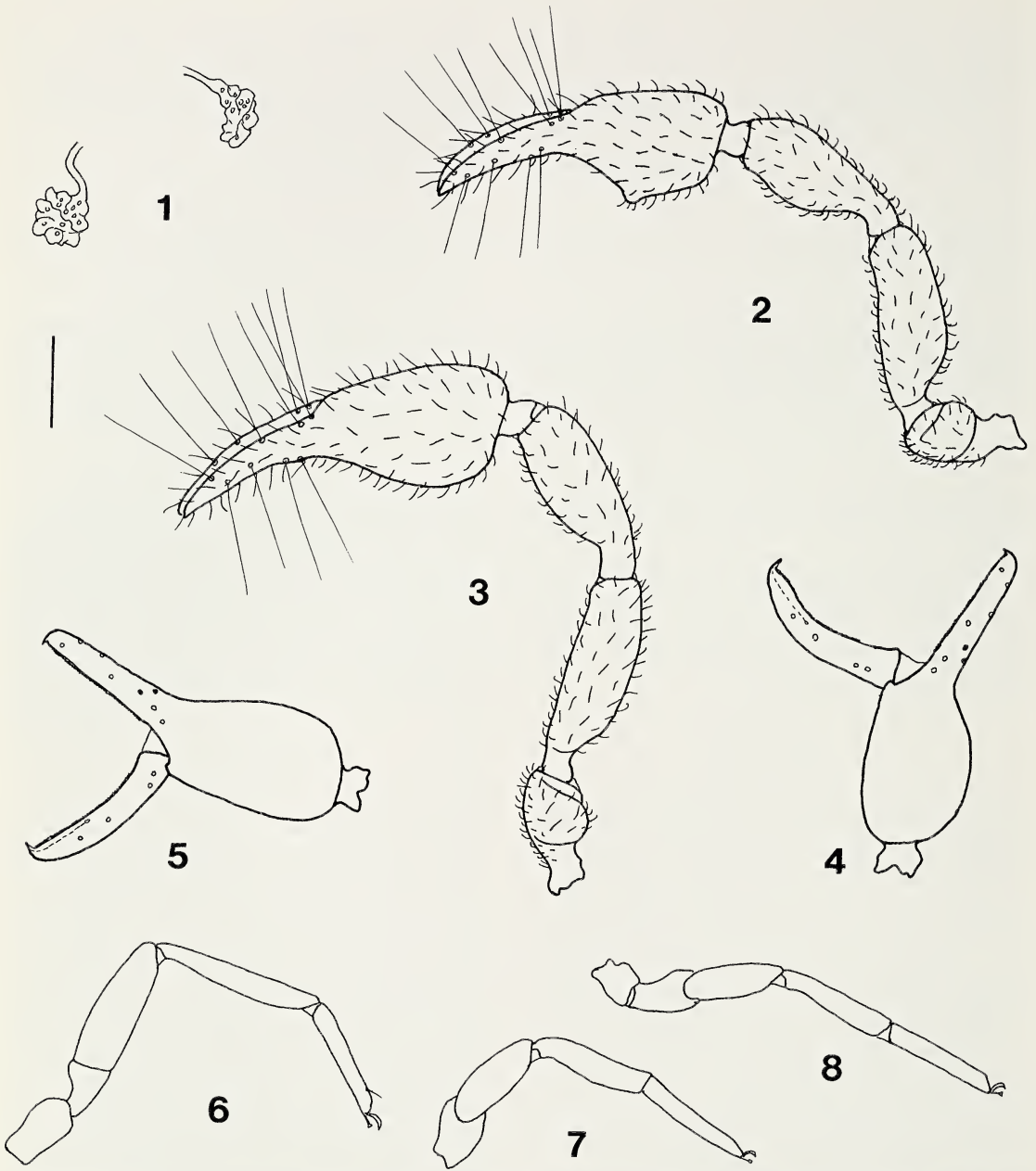
Figs. 1–8

**Type data.**—Holotype male (WM7269.02005), female paratype (allotype) (WM7269.02008), and about 180 other paratypes (including all stages) taken in ethylene glycol pitfall traps in Poleta Cave, Westgard Pass, Inyo-White Mountains, Inyo County, California, 21 May–5 November 1988, R. Aalbu; holotype, allotype and 28 paratypes (all stages) mounted on slides. Three paratypes (2♀, 1 tritonymph) taken in antifreeze pitfall trap in Poleta Cave (as “Westgard Pass Cave”), 27 May–26 November 1982, D. Giuliani; mounted on slides. All mounted specimens in FSCA, some alcoholic specimens in CAS.

**Diagnosis.**—Much like *T. ubicki* new species, but specimens larger, palp and leg IV less stout. Tarsus of leg I in *T. aalbei* new species male more similar to that of conspecific female than is the case in *T. ubicki*.

**Description.**—Male and female similar in most respects, but female usually a little larger, and palpal chelae and first legs sexually dimorphic. Palps reddish-brown, carapace light brown, chelicerae and legs tan. Carapace longer than broad; surface granulate, with two distinct transverse furrows; no eyes; about 80

clavodentate setae, 4 at anterior and 12–16 at posterior margin. Abdominal tergites 1–10 and sternites 4–10 divided; surfaces of tergites lightly granulate; pleural membranes irregularly longitudinally striate; most dorsal setae slender and clavodentate, ventral setae very slender and denticulate or clavodentate. Tergal chaetotaxy of holotype 18:23:21:25:28:26:25:24:24:22:T12T:2, others similar; tactile setae (T) apparently very fragile, as they are usually missing from their areoles. Sternal chaetotaxy of holotype (male) ~50:[33]:(2)29(1):(2)6(2):16:21:21:21:21:18:T1T2T1T:2, other males similar; anterior chaetotaxy of allotype (female) 32:(2)14(2):(3)6(4):14:21:–, other females similar. Internal genitalia of male typically chernetid in form, fairly large and well sclerotized. Spermathecae of female are long tubes with irregular, ovoid end sacs (Fig. 1); the tubes must be thin-walled and fragile, as none could be followed to a medial atrium. Chelicera 0.3 as long as carapace; hand usually with 6 setae (occasionally 5), *bs*, *sbs*, and *xs* terminally denticulate, others acuminate; flagellum of 4 setae, the distal 2 long and anteriorly serrate, the proximal 2 short and terminally denticulate; galea slender, with 5–6 small rami, equally developed in male and female. Palp (Figs. 2, 3) rather long, stouter in male than in female: (numbers for male followed in parentheses by those for female): femur 0.85–0.92 (0.9–1.0) and chela about 1.25 (1.35–1.45)× as long as carapace; L/B of trochanter 1.65–1.95 (1.85–2.15), femur 3.0–3.25 (3.45–3.65), patella 2.65–2.8 (2.8–3.1), and chela (without pedicel) 2.5–2.8 (2.8–3.1); L/D of hand (without pedicel) 1.4–1.55 (1.5–1.7); movable finger L/hand L 0.95–1.1. Chela of male quite robust, with a conspicuous, conical protuberance on medial side of hand, and with movable finger distinctly bowed (Fig. 4); chela of female more slender and without these features. Surfaces lightly granulate; most setae narrow clavodentate. Trichobothria as shown in Figs. 4, 5. Each finger with 45–50 contiguous, cusped marginal teeth; fixed finger with 9–11 external and 3–6 internal, and movable finger with 5–10 external and 1–2 internal accessory teeth. Venom apparatus present only in movable finger, nodus ramosus between trichobothria *t* and *st*. Legs slender: leg IV (Fig. 6) with L/D of femur+patella 4.4–4.85, tibia 7.0–7.8, and tarsus 6.35–7.45. Leg I of male (Fig. 7) with tarsus slightly



Figures 1-8.—*Tuberochernes aalbui* new species. 1, Spermathecae of allotype female; 2, Right palp of holotype male, dorsal view; 3, Right palp of allotype female, dorsal view; 4, Left chela of paratype male, lateral view, showing trichobothriotaxy (all setae omitted; darkened areoles are underneath); 5, Left chela of allotype female; 6, Leg IV of holotype male (vestitural setae omitted); 7, Leg I of holotype male. 8, Leg I of allotype female. Scale bar = 0.15 mm for Fig. 1, and 0.5 mm for all others.

bowed, concave dorsally; that of female (Fig. 8) normal, straight. Leg IV with a short tactile seta on tarsus 0.75-0.8 length of segment from proximal end; these setae are variably acuminate or terminally denticulate.

*Nymphs:* Generally similar to adults, but progressively smaller, lighter in color, and with appendages slightly more robust. Hand of chelicera with fewer setae: tritonymph with 5 or 6 (*xs* sometimes absent), deutonymph



with 5 (*xs* absent), and protonymph with 4 (*xs* and *bs* absent); flagellum with 4 setae in all stages. Palp: fixed and movable fingers bear the typical numbers of trichobothria for each stage. Leg IV: tarsus bears a short, acuminate tactile seta 0.65–0.7 length of segment from proximal end.

**Measurements.**—*Male*: Figures given first for holotype, followed in parentheses by ranges for seven paratypes. Body L 4.22 (3.85–4.68). Carapace L 1.30 (1.21–1.35). Chelicera L 0.37 (0.37–0.42). Palp: trochanter 0.63 (0.62–0.695)/0.34 (0.325–0.38); femur 1.13 (1.06–1.23)/0.355 (0.34–0.41); patella 1.01 (1.00–1.11)/0.37 (0.37–0.415); chela (without pedicel) 1.61 (1.56–1.70)/0.59 (0.555–0.665); hand (without pedicel) 0.815 (0.82–0.92)/0.555 (0.53–0.62); pedicel L 0.15 (0.13–0.16); movable finger L 0.89 (0.83–0.925). Leg I: femur+patella L 0.83 (0.815–0.90); femur 0.455 (0.43–0.48)/0.235 (0.235–0.265); patella 0.58 (0.56–0.62)/0.19 (0.19–0.23); tibia 0.67 (0.64–0.75)/0.13 (0.14–0.16); tarsus 0.615 (0.57–0.70)/0.105 (0.09–0.11). Leg IV: femur+patella 1.02 (0.97–1.10)/0.23 (0.215–0.245); tibia 0.92 (0.865–1.02)/0.125 (0.125–0.14); tarsus 0.665 (0.615–0.74)/0.105 (0.095–0.11).

*Female*: Figures given first for allotype, followed in parentheses by ranges for 12 paratypes. Body L 4.40 (3.65–4.85). Carapace L 1.29 (1.16–1.34). Chelicera L 0.39 (0.355–0.41). Palp: trochanter 0.665 (0.615–0.69)/0.32 (0.29–0.34); femur 1.18 (1.07–1.24)/0.34 (0.30–0.36); patella 1.06 (0.955–1.11)/0.38 (0.34–0.415); chela (without pedicel) 1.85 (1.61–1.88)/0.62 (0.525–0.635); hand (without pedicel) 0.95 (0.83–1.01)/0.585 (0.51–0.62); pedicel L 0.13 (0.11–0.13); movable finger L 0.93 (0.83–0.955). Leg I: femur+patella L 0.835 (0.74–0.87); femur 0.42 (0.36–0.45)/0.215 (0.185–0.22); patella 0.56 (0.52–0.605)/0.18 (0.16–0.19); tibia 0.65 (0.58–0.70)/0.125 (0.11–0.125); tarsus 0.63 (0.58–0.69)/0.095 (0.09–0.095). Leg IV: femur+patella 1.07 (0.985–1.13)/0.22 (0.205–0.245); tibia 0.955 (0.865–1.04)/0.13 (0.11–0.13); tarsus 0.70 (0.635–0.725)/0.095 (0.09–0.105).

*Tritonymph*: Ranges for five paratypes. Body L 2.85–3.30. Carapace L 0.89–1.05. Chelicera L 0.28–0.325. Palp: trochanter 0.445–0.52/0.22–0.27; femur 0.725–0.89/0.235–0.29; patella 0.635–0.785/0.265–0.325;

chela (without pedicel) 1.23–1.43/0.435–0.50; hand (without pedicel) 0.63–0.73/0.43–0.495; pedicel L 0.08–0.09; movable finger L 0.665–0.74. Leg IV: femur+patella 0.69–0.82/0.16–0.19; tibia 0.57–0.665/0.105–0.12; tarsus 0.45–0.525/0.08–0.09.

*Deutonymph*: Ranges for three paratypes. Body L 1.95–2.25. Carapace L 0.615–0.67. Chelicera L 0.20–0.25. Palp: trochanter 0.30–0.35/0.15–0.18; femur 0.47–0.55/0.15–0.185; patella 0.42–0.48/0.17–0.215; chela (without pedicel) 0.83–0.96/0.26–0.325; hand (without pedicel) 0.415–0.495/0.26–0.31; pedicel L 0.05–0.07; movable finger L 0.46–0.495. Leg IV: femur+patella 0.445–0.525/0.12–0.135.

*Protonymph*: Ranges for three paratypes. Body L 1.45–1.75. Carapace L 0.48–0.56. Chelicera L 0.185–0.19. Palp: trochanter 0.235–0.245/0.12–0.125; femur 0.34–0.355/0.115–0.125; patella 0.31/0.13–0.14; chela (without pedicel) 0.615–0.65/0.18–0.20; hand (without pedicel) 0.32–0.33/0.18–0.19; pedicel L 0.04; movable finger L 0.325–0.35.

**Etymology.**—The species is named in honor of Rolf Aalbu, who collected most of the type specimens.

**Remarks.**—The first legs of the male are somewhat modified compared to those of the female, though not so much so as in *T. ubicki* (see below).

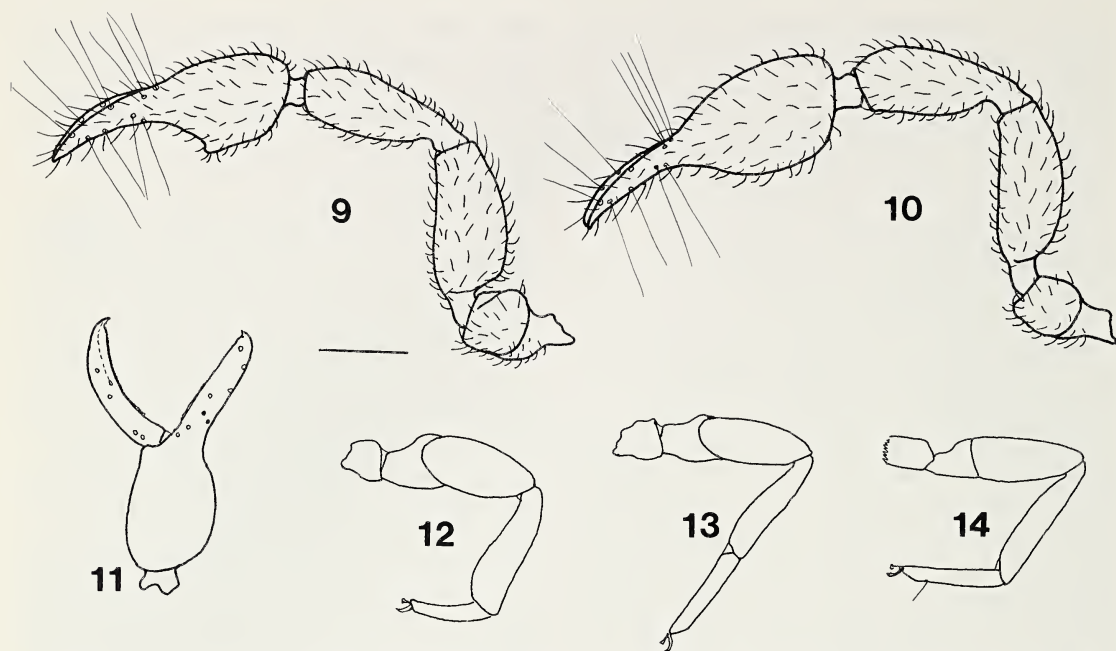
#### *Tuberochernes ubicki* new species

Figs. 9–14

**Type data.**—Holotype male (WM7729.01001) and female paratype (allotype) (WM7729.01002) from under stones in Fly Cave, Gardner Canyon, Santa Rita Mountains, Santa Cruz County, Arizona, 24 June 1988, D. Ubick; mounted on slides, in CAS.

**Diagnosis.**—Much like *T. aalbui*, but a little smaller, with palp and leg IV a little stouter, and leg I of male apparently raptorial, the segments being distinctly modified.

**Description.**—Male and female generally similar, but female a little larger, and palpal chelae and first legs sexually dimorphic. Palps reddish-brown, carapace light brown, chelicerae and legs tan, other parts lighter. Carapace longer than broad; surface covered with low granules and with two distinct, transverse furrows; no eyes; about 90–100 clavodentate setae, 4 at anterior and 18–20 at posterior margin. Abdominal tergites 2–10 and sternites 4–10 divided; surface of tergites lightly granulate;



Figures 9-14.—*Tuberochernes ubicki* new species. 9, Right palp of holotype male, dorsal view; 10, Right palp of allotype female, dorsal view; 11, Left chela of holotype male, lateral view, showing trichobothriotaxy (all setae omitted; darkened areoles are underneath); 12, Leg I of holotype male (vestitural setae omitted); 13, Leg I of allotype female; 14, Leg IV of holotype male. Scale bar = 0.5 mm.

pleural membranes irregularly longitudinally striate; most dorsal setae slender, clavodentate, ventral setae slender, acuminate to clavodentate. Tergal chaetotaxy of holotype 20:28:26:28:27:29:30:26:23:21:T12T:2. Sternal chaetotaxy of holotype (male) 60:[4-4]:(1)25(1):(1)6(1):15:20:20:20:20:18:T2T2T1T:2; anterior chaetotaxy of allotype (female) 34:(1)9(1):(1)5(1):16:22:—. Internal genitalia of male typically chernetid in form; spermathecae of female not clear, but apparently like those of *T. aalbui* new species. Chelicera 0.25 as long as carapace; hand with 6 setae, *is* and *ls* long, acuminate, others rather short and terminally denticulate; flagellum of 4 setae, distal 2 long and serrate, proximal 2 short and denticulate near tip; galea of male small, with 3-4 spinules, that of female longer, slender, with 6 small rami. Palp rather robust (Figs. 9, 10): (numbers for male followed in parentheses by those for female). Femur 0.9 (0.95) and chela 1.15× (1.35) as long as carapace. L/B of trochanter 1.5 (1.85), femur 2.6 (2.95), patella 2.8 (2.7), and chela (without pedicel) 2.7 (2.7); L/D of hand (without pedicel) 1.55 (1.45); movable finger L / hand L 1.15 (0.95). Chela sexually dimorphic; that of male more robust,

with a conical protuberance on medial side of hand, and with movable finger distinctly bowed (Fig. 11); that of female more slender, without a protuberance on hand, and with movable finger only gently curved. Surfaces granulate; most setae clavodentate. Trichobothria as shown in Fig. 11. Fixed finger with about 45 and movable finger with 45-50 cusped marginal teeth, and 1-3 internal and 7-9 external accessory teeth. Venom apparatus developed only in movable finger. Legs more robust than those of *T. aalbui*: leg IV (Fig. 14) with L/D of femur+patella 3.8 and tibia 6.0. Leg I sexually dimorphic: that of male apparently raptorial, with robust femur, patella and tibia, and elongate, curved tarsus (Fig. 12), L/D of femur+patella 2.75 and tibia 3.6; leg I of female normal, slender (Fig. 13), L/D of femur+patella 3.35 and tibia 4.55. Tarsus of leg IV with a short acuminate or denticulate tactile seta 0.75 length of segment from proximal end.

**Measurements.**—Figures given first for holotype male, followed in parentheses by those for allotype female. Body L 3.55 (4.12). Carapace L 1.18 (1.20). Chelicera L 0.30 (0.355). Palp: trochanter 0.63 (0.605)/0.385 (0.325); femur 1.04 (1.10)/0.40 (0.37); patella



0.99 (1.02)/0.35 (0.38); chela (without pedicel) 1.36 (1.60)/0.50 (0.59); hand (without pedicel) 0.69 (0.85)/0.45 (0.585); pedicel L 0.13 (0.12); movable finger L 0.78 (0.82). Leg I: femur+patella L 0.895 (0.925); femur 0.38 (0.33)/0.31 (0.215); patella 0.63 (0.525)/0.30 (0.20); tibia 0.755 (0.59)/0.21 (0.13); tarsus 0.47 (0.495)/0.09 (0.08). Leg IV: femur+patella 0.895 (0.925)/0.235 (0.24); tibia 0.835 (0.835)/0.14 (0.13); tarsus 0.58 (0.59)/0.095 (0.095).

**Etymology.**—The species is named for Darrell Ubick, who collected the type specimens.

**Remarks.**—The first legs of the male look as though they might be very useful in seizing or holding prey, but there is no direct evidence that this is so. They might, rather, be used in grasping the female during courtship and sperm transfer, which, in some chernetid pseudoscorpions, can involve rather complex maneuvers (see Weygoldt 1969).

## DISCUSSION

Several other genera of chernetid pseudoscorpions have medial protuberances on the palpal chela. *Tuberochernes* is easily distinguished from *Mirochernes* Beier 1930 (from eastern U.S.), in which the male has a very large, distally directed, hooklike process (Hoff 1949: fig. 45C). And it differs from *Interchernes* Muchmore 1980 (from Baja California, Mexico), where the process is a small, discrete, conical nubbin located at the base of the fixed finger and is present in both sexes (Muchmore 1980). *Bituberochernes* Muchmore 1974 (from Florida and the West Indies), likewise, has a small process at base of the fixed finger, but it differs fundamentally from *Tuberochernes* in having a three-bladed cheliceral flagellum, distinctive female genitalia, and highly specialized setae on leg I of the male (see Muchmore 1974b, 1979). *Petterchernes* Heurtault 1986 (from Brazil), with a large hump on the chelal hand, has a three-bladed flagellum, and broad, leaflike setae (Heurtault 1986). No other chernetid pseudoscorpions are known to have protuberances on the chelal hand. *Cordylochernes octentoctus* (Balzan 1891) (from South Africa?) was originally illustrated as having a triangular tubercle on the base of the fixed chelal finger (Balzan 1891: fig. 5); however, Vachon (1942), on reexamination of the unique type of the spe-

cies, found that the protuberance was actually a bit of foreign material stuck to the surface of the finger.

Of the genera mentioned above, *Tuberochernes* is more closely related to *Mirochernes* and *Interchernes*, in the possession of a four-bladed flagellum, paired, long, slender, tubular spermathecae, and other characters (see Muchmore 1974a). In these characters also, it is close to *Chernes* Menge 1855, *Dinocheirus* Chamberlin 1929 and *Hesperochernes* Chamberlin 1924, all widely distributed in the United States.

In addition to the distinctive medial protuberance on the chelal hand, males of *Tuberochernes* have a uniquely modified leg I (more so in *T. ubicki* than in *T. aalbui*). All segments of the first legs are more robust than in females and the tarsus is curved, so that, in *T. ubicki* especially, it appears useful for seizing or grasping. The exact nature of the modifications of the anterior appendages is not known, but, as they are found only in the males, it might be supposed that they are somehow related to courtship and mating. On the other hand, known species of the genus are found only in caves, and these may be adaptations to some aspect of life in that habitat.

Though it is common in cheliferid pseudoscorpions, sexually dimorphic modification of the first legs is rare in chernetids. Representatives of only three chernetid genera have been known previously to be so modified, namely, *Pachychernes* Beier 1932 from South and Central America, *Orochernes* Beier 1968 from Nepal and Siberia and *Bituberochernes* Muchmore 1974 from Florida and the West Indies (see Muchmore 1996). In all of these, the modifications involve the occurrence of very long, or short, specialized, setae, which are not present in *Tuberochernes* species.

Representatives of *Tuberochernes* are presently known only from caves at moderately high elevations, *T. aalbui* in Poleta Cave, Westgard Pass, White-Inyo Mountains, Inyo County, California, at about 2200 m elevation, and *T. ubicki* in Fly Cave, Gardner Canyon, Santa Rita Mountains, Santa Cruz County, Arizona, at about 1600 m. The widely separated and restricted localities of *T. aalbui* and *T. ubicki* in California and Arizona strongly suggest that these species are relicts of a formerly widespread ancestral population, fragmented

by desertification in the intervening areas. Similar disjunct patterns of distribution in California and Arizona have been observed in several other groups of arachnids: the antrodiaetid spiders *Aliatypus janus* Coyle 1974 and *A. isolatus* Coyle 1974 (see Coyle 1974); the vaejovid scorpions *Uroctonites giulianii* Williams & Savary 1991 and *U. huachuca* (Gertsch & Sologlad 1972) (see Williams & Savary 1991); the hubbardiid schizomids *Hubbardia borregoensis* (Briggs & Hom 1966) and *H. wessoni* (R.V. Chamberlin 1939) (see Reddell & Cokendolpher 1995); two species of the phalangodid harvestman genus *Sitalcina* Banks 1911 (Ubick & Briggs, unpubl.); and others. It will not be surprising if additional representatives of *Tuberochernes* are found in other montane or subterranean refugia in California and Arizona.

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## NEW SPECIES OF CHTHONIIDAE AND NEOBISIIDAE (ARACHNIDA, PSEUDOSCORPIONES) FROM MONTENEGRO, YUGOSLAVIA

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**ABSTRACT.** The pseudoscorpions of the genera *Chthonius* C.L. Koch 1843 (Chthoniidae) and *Roncus* L. Koch 1873 (Neobisiidae) from Montenegro, Yugoslavia have been studied. Three new species, *Chthonius* (*Chthonius*) *prove*, *Roncus hors*, and *R. davor* are described. Diagnostic characters of the analyzed taxa are thoroughly described and figured. Taxonomic interrelationships and geographical distribution are briefly discussed. Including these three species, the family Chthoniidae occurs with five species in Montenegro, the family Neobisiidae with 13 species.

Only two cave (troglophilic) species of *Chthonius* C.L. Koch 1843 (subgenus *Chthonius* s. str.) (Chthoniidae) are presently known from Montenegro, Yugoslavia, viz. *C. (C.) exarmatus* Beier 1939 and *C. (C.) porevid* Ćurčić, Dimitrijević & Makarov 1996; the former species inhabits a cave on Mt. Orjen, while the latter populates the Knezlaz Pećina Cave, Krivošije, Mt. Orjen, near Risan (Ćurčić et al. 1996b). To date, only two pseudoscorpions of the genus *Roncus* L. Koch 1873 (Neobisiidae) are known to inhabit Montenegro (Ćurčić et al. 1996a,b). These are: *Roncus yaginumai* Ćurčić, Ćurčić & Dimitrijević 1996, from a cave on the isle of Vranjina, near Podgorica, and *R. belbog* Ćurčić, Dimitrijević & Makarov 1996, from the Knezlaz Pećina Cave (also the type-locality of *C. (C.) porevid*) (Ćurčić et al. 1996a, b).

The aim of this study is to present descriptions of three new species (one of *Chthonius* and two of *Roncus*), as well as to define their precise taxonomic status. With the new species described in the present study, the total number of the Chthoniidae inhabiting Montenegro is now five, and of the Neobisiidae — 13 species (Ćurčić 1974, 1988).

### METHODS

In the present study, material from three samples of pseudoscorpions collected in 1991 and 1992 has been examined. The first sample from a cave in the village Gornji Morinj, near

Risan, Montenegro (Yugoslavia), contained two new taxa: *Chthonius* (*Chthonius*) *prove* new species, and *Roncus hors* new species. The other two samples from Mt. Durmitor (from the canyon of the Sušica River and the village of Tepca, 1000–1100 m elev.), Montenegro (Yugoslavia), contained another undescribed species: *Roncus davor* new species. The new species described in this paper are probably endemic forms inhabiting either caves (*C. prove* new species and *R. hors* new species) or epigean habitats (*R. davor* new species). All studied pseudoscorpion specimens were mounted on slides in Swan's fluid (gum chloral medium) and deposited in the collections of the Institute of Zoology, Faculty of Biology, University of Belgrade, Yugoslavia. All trichobothrial designations are in accordance with Beier (1932). Terminology for pedipalpal and pedal podomeres follows Harvey (1992).

### CHTHONIIDAE Daday 1888

*Chthonius* (*Chthonius*) *prove* new species  
Figs. 1–5; Table 1

**Etymology.**—In Slav mythology, *Prove* is the deity of justice (Petrović 1995).

**Specimen examined.**—Holotype female, from a cave in the village Gornji Morinj, near Risan, Montenegro, Yugoslavia; 27 June 1991 (collected by I.M. Karaman, together with the holotype male of *Roncus hors* new species).

**Description.**—Carapace slightly longer than wider (almost quadrangular); epistome differentiated (Fig. 4). Neither eyes nor eye-spots developed. Setal formula:  $m4m+6+4+2+4 = 22$  setae (a single microseta in the preocular recess on either side). A pair of posterior and lateral setae of unknown size (broken). Carapace pale-yellowish and transparent.

Tergites I-X and sternites IV-X smooth, entire and uniseriate. Tergal formula: 4-4-4-6-6-6-6-6-6-6. Female genital area: sternite II with 8 setae clustered medially and posteriorly in the form of a triangle. Sternite III with 8 setae and 3 suprastigmatic microsetae along each stigma. Sternite IV with 7 posterior setae and 3 microsetae on either side. Sternites V-X each with 8–10 setae. Male genital area: unknown. Pleural membranes granulostriate.

Cheliceral spinneret (galea) in the form of a small sclerotic tubercle (Fig. 5). Cheliceral palm with six setae and two or three accessory microsetae, movable finger with one seta. Fixed cheliceral finger with two distal large teeth and a row of eight pointed and contiguous teeth which diminish in size proximally. Movable cheliceral finger with a small isolated tooth (just below the level of the galea), one large tooth, and a series of 12 triangular teeth, slightly asymmetrical and diminishing in size proximally. Dentition of cheliceral fingers as in Fig. 5. Galeal seta inserted basal to the teeth of the movable cheliceral finger. Flagellum of 11 blades, one small blade proximally and 10 blades twice this length, more or less in pairs, distally. The most distal members of the series are curved but all, to some extent, are pinnate on two sides.

Manducatory process (apex of pedipalpal coxa) with two long setae, pedipalpal coxa with three setae. Trochanter short, other pedipalpal articles moderately elongate (Figs. 1, 2). Chelal fingers of almost equal size. Fixed chelal finger is slightly S-shaped, and the movable finger is somewhat curved inwards, or C-shaped (Fig. 2). Tip of fixed finger (distal to *et*) bears 2 or 3 small distal teeth. Fixed chelal finger with 29 triangular teeth which occupy almost the whole length of the finger blade; distal and proximal members of this series are close-set, whilst the median teeth are spaced and slightly asymmetrical. Movable chelal finger with 16–18 teeth; distal and median members are inclined backwards, and

these are followed by small, low and asymmetrical teeth; at the level of *b-sb*, these teeth merge into a dental lamella. Chelal fingers are longer than chelal palm, and pedipalpal femur is slightly shorter than chelal fingers, but almost as long as carapace (Table 1).

Trichobothriotaxy: *ib* and *isb* on chelal palm; fixed chelal finger with a further six trichobothria (*et*, *est*, *esb*, *eb*, *it*, and *ist*, and a pair of accessory setae nearer to *et* than to the finger tip); movable chelal finger bears four trichobothria (*t*, *st*, *sb*, and *b*). Seta *esb* distal to *eb*, *ist* closer to *esb* than to *eb* and distal to the former; *it* close to *est*; *it-est* at the level of *t-st*; *et* close to accessory setae. Seta *sb* closer to *b* than to *st*; *st* nearer to *t* than to *sb*. Distance *st-sb* is almost  $1.8\times$  as long as *b-sb*; distance *t-st* more than  $8\times$  as long as *sb-st*. Seta *b* at the level of *ist* (Fig. 2).

Coxa II bears 7 or 8 spines, and coxa III has 3 or 4 spines which are elongate and finely pinnate on two sides. Intercoxal tubercle with two small setae. Tibia IV, metatarsus IV, and tarsus IV each with a long tactile seta.

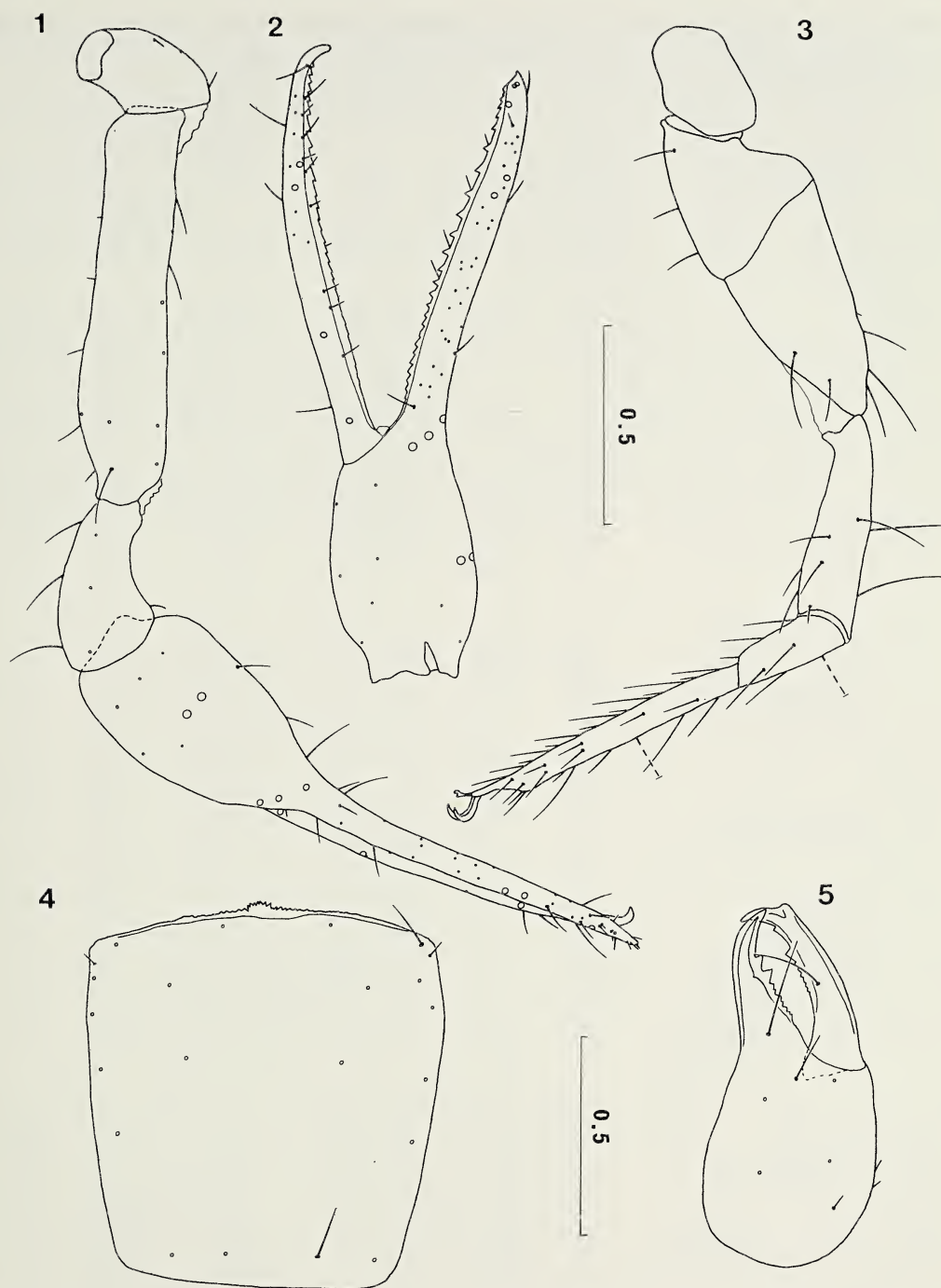
The whole specimen is depigmented and delicate in appearance. Measurements and morphometric ratios are presented in Table 1.

**Distribution.**—South Montenegro, Yugoslavia, in a cave; probably endemic species.

**Diagnosis.**—This new species is phenetically most similar to *C. (C.) ischnocheles reductus* Beier 1939, from the Jama Pothole on the island of Giuppana (Šipun), Croatia, as well as to *C. (C.) absoloni* Beier 1939, from the Dužice Pećina near Trebinje, south Hercegovina, Bosnia-Hercegovina. From *C. (C.) ischnocheles reductus*, *C. (C.) prove* is easily distinguished by the color of the body (yellow, with reddish-brown appendages vs. pale, almost transparent), in the presence/absence of eyes (present vs. absent), in the carapacial setation (18 vs. 22 setae), in the setal formula of tergites I-X (4-4-4-4-6-6-6-6-4-4 vs. 4-4-4-6-6-6-6-6-6-6), in the pedipalpal chelal length to breadth ratio of females (5.00 vs. 4.055), in the number of teeth on the fixed chelal finger of females (48 vs. 29), in the pedipalpal chelal length of females (0.92 mm vs. 0.73 mm).

The new species is clearly distinct from *C. (C.) absoloni* in a number of morphological traits: the carapacial setation (22 vs. 18 setae),





Figures 1–5.—*Chthonius (Chthonius) prove* new species, holotype female. 1, Pedipalp (trichobothria omitted); 2, Pedipalpal chela (trichobothria omitted); 3, Leg IV; 4, Carapace; 5, Chelicera. Scale lines in mm.

Table 1.—Linear measurements (in mm) and selected morphometric ratios in *Chthonius* (*Chthonius*) *prove* new species, *Roncus hors* new species and *Roncus davor* new species, all from Montenegro, Yugoslavia. Abbreviations: TS = tactile seta, T = tritonymph, D = deutonymph.

Character	C. (C.)		♀ ♀	R. davor ♂ ♂	T	D
	<i>prove</i> ♀	<i>R. hors</i> ♂				
Body						
Length (1)	1.58	2.04	2.445–3.18	2.30–2.75	2.13	1.63
Cephalothorax						
Length (2)	0.51	0.60	0.64–0.73	0.48–0.69	0.55	0.40
Breadth	0.48	0.51	0.58–0.66	0.45–0.62	0.38	0.38
Abdomen						
Length	1.07	1.44	1.715–2.54	1.82–2.06	1.58	1.23
Breadth	0.64	0.69	0.96–1.31	0.86–0.99	0.75	0.58
Chelicerae						
Length (3)	0.46	0.35	0.40–0.48	0.40–0.425	0.34	0.25
Breadth (4)	0.27	0.25	0.22–0.24	0.23–0.24	0.18	0.12
Length of movable finger (5)	0.24	0.18	0.27–0.33	0.28	0.23	0.15
Length of galea	0.01	0.005	0.01	0.01	0.005	0.003
Pedipalps						
Length with coxa (6)	2.03	2.90	3.245–3.845	3.52–3.64	2.53	1.70
Length of coxa	0.31	0.48	0.55–0.61	0.51–0.55	0.425	0.25
Length of trochanter	0.23	0.36	0.38–0.47	0.44–0.45	0.32	0.22
Length of femur (7)	0.52	0.58	0.60–0.795	0.70–0.71	0.53	0.33
Breadth of femur (8)	0.12	0.18	0.205–0.25	0.20–0.22	0.16	0.13
Ratio 7/8	4.33	3.22	2.93–3.18	3.23–3.50	3.31	2.54
Ratio 7/2	1.02	0.97	0.94–1.09	1.03–1.46	0.96	0.825
Length of patella (tibia) (9)	0.24	0.48	0.555–0.64	0.57–0.62	0.41	0.27
Breadth of patella (tibia) (10)	0.13	0.22	0.26–0.33	0.27–0.28	0.195	0.14
Ratio 9/10	1.85	2.18	1.94–2.13	2.11–2.21	2.10	1.93
Length of chela (11)	0.73	1.00	1.16–1.33	1.30–1.31	0.845	0.63
Breadth of chela (12)	0.18	0.28	0.41–0.46	0.38–0.40	0.275	0.195
Ratio 11/12	4.055	3.57	2.83–2.89	3.275–3.42	3.07	3.06
Length of chelal palm (13)	0.27	0.46	0.52–0.64	0.59–0.63	0.40	0.31
Ratio 13/12	1.50	1.64	1.27–1.39	1.55–1.575	1.45	1.59
Length of chelal finger (14)	0.55	0.54	0.64–0.69	0.68–0.71	0.445	0.32
Ratio 14/13	2.04	1.17	1.08–1.23	1.08–1.20	1.11	1.03
Leg IV						
Total length	1.595	2.08	2.395–2.68	2.51	1.84	1.085
Length of coxa	0.22	0.36	0.40–0.47	0.38	0.34	0.20
Length of trochanter (15)	0.18	0.27	0.31–0.34	0.33	0.22	0.16
Breadth of trochanter (16)	0.12	0.12	0.13–0.17	0.17	0.10	0.09
Ratio 15/16	1.50	2.25	2.00–2.38	1.94	2.20	1.78
Length of femur + patella (17)	0.45	0.54	0.62–0.72	0.65	0.47	0.26
Breadth of femur + patella (18)	0.19	0.19	0.20–0.27	0.24	0.185	0.11
Ratio 17/18	2.37	2.84	2.67–3.10	2.71	2.54	2.36
Length of tibia (19)	0.30	0.46	0.535–0.59	0.58	0.40	0.205
Breadth of tibia (20)	0.085	0.10	0.11–0.12	0.13	0.10	0.075
Ratio 19/20	3.53	4.60	4.86–4.92	4.46	4.00	2.73
Length of metatarsus (21)	0.14	0.17	0.19–0.23	0.22	0.16	0.10
Breadth of metatarsus (22)	0.07	0.075	0.08	0.09	0.08	0.06
Ratio 21/22	2.00	2.27	2.375–2.875	2.44	2.00	1.67
Length of tarsus (23)	0.305	0.28	0.33–0.34	0.35	0.25	0.16
Breadth of tarsus (24)	0.04	0.06	0.075–0.08	0.08	0.07	0.06



Table 1.—Continued.

Character	<i>C. (C.)</i>		♀ ♀	<i>R. davor</i> ♂ ♂	T	D
	<i>prove</i> ♀	<i>R. hors</i> ♂				
Ratio 23/24	7.625	4.67	4.125–4.53	4.375	3.57	2.67
TS ratio—tibia IV	0.53	0.59	0.54–0.56	0.61	0.54	0.43
TS ratio—metatarsus IV	0.43	0.26	0.16–0.285	0.23	0.21	0.32
TS ratio—tarsus IV	0.26	0.31	0.32–0.35	0.37	0.33	0.36

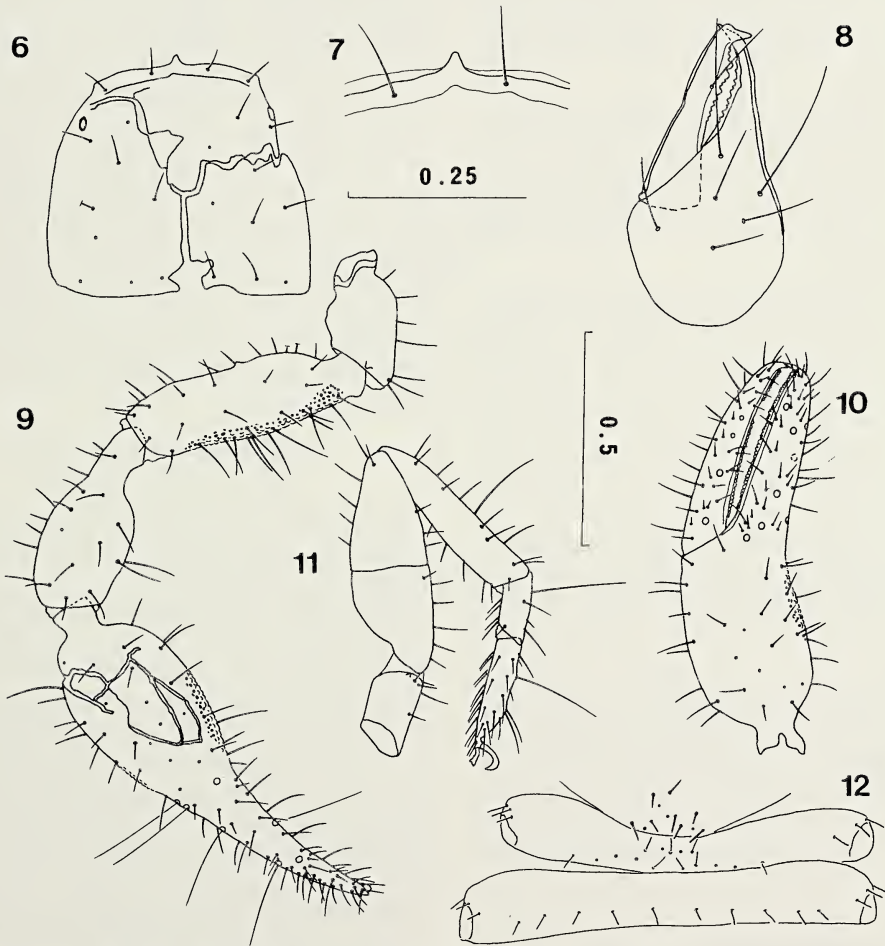
the setation of tergites I–V (4–4–4–6–6 vs. 4–4–4–4–6), in the pedipalpal chelal length to breadth ratio of females (4.055 vs. 5.80), in the number of spines on coxae II of females (7 or 8 vs. 5), in the form of both pedipalpal chelal palm and chelal finger (less elongate vs. more elongate) (Fig. 2; Beier 1939, fig. 3).

Neobisiidae J.C. Chamberlin 1930

*Roncus hors* new species  
Figs. 6–12; Table 1

**Etymology.**—In Slav mythology, *Hors* is the God of Sun (Petrović 1995).

**Specimen examined.**—Holotype male,



Figures 6–12.—*Roncus hors* new species, holotype male. 6, Carapace; 7, Epistome; 8, Chelicera; 9, Pedipalp; 10, Pedipalpal chela (trichobothria omitted); 11, Leg IV; 12, Genital area. Scales in mm.

from a cave in the village Gornji Morinj, near Risan, Montenegro, Yugoslavia; 27 June 1991 (collected by I.M. Karaman, together with the holotype female of *C. (C.) prove* new species).

**Description.**—Epistome small (but distinct), triangular and apically rounded (Figs. 6, 7). A single pair of eyes developed; eye lenses somewhat reduced and flattened. Setal formula:  $4+7+5+1+6 = 23$  setae (male) (Fig. 6). Carapace reticulate throughout.

Abdominal tergite setal formula (I-X): 6-9-11-11-11-11-11-10-10-10. Both tergites I-X and sternites IV-X entire, uniseriate, and smooth. Twelfth abdominal segment with two pairs of small setae. Female genital area: unknown. Male genital area: sternite II with 12 long median and posterior setae (of these, 6 setae are retromarginal); sternite III with 5 (3+2) anterior, 10 posterior setae, and 3 suprastigmatic setae on either side; sternite IV with 10 posterior setae and 3 microsetae along each stigma. Sternites V-X with 13-15-14-13-13-13 setae.

Galea distinct, low and rounded. Cheliceral palm with 6, movable finger with one seta (Fig. 8). Cheliceral dentition as in Fig. 8. Flagellum with one short proximal blade and seven longer blades distally, characteristic of the genus *Roncus*.

Apex of pedipalpal coxa (manducatory process) with four long setae. Pedipalpal trochanter with a small tubercle. A small exterolateral tubercle on pedipalpal femur present; pedipalpal femur and chelal palm with interior granulations, patella (tibia) smooth (Fig. 9). A single tiny tubercle present on the interolateral side of the chelal palm. No group of microsetae proximal to trichobothria *eb* and *esb*; instead, some small setae distal to *eb* and *esb* (6-8) present. Fixed chelal finger with 47 small, asymmetrical, and close-set teeth; movable finger with 47 small and contiguous teeth. Chelal fingers longer than chelal palm and only slightly shorter than pedipalpal femur (Table 1). Trichobothrial pattern: *ist* slightly closer to *est* than to *isb*; *sb* equidistant from *b* and *st*; *st* closer to *t* than to *sb*. Distribution of trichobothria as illustrated in Fig. 10.

Leg IV: tibia, metatarsus, and tarsus each with a long tactile seta.

Morphometric ratios and linear measurements are presented in Table 1.

**Distribution.**—South Montenegro, Yugoslavia, in a cave; probably endemic species.

**Diagnosis.**—This new species is easily distinguished from its phenetically similar congener, *R. yaginumai*, by the setation of the carapace (23 vs. 24-27 setae), by the form of the pedipalpal podomeres (stout vs. elongate) (Figs. 9, 10) (Ćurčić et al. 1996a), by the number of teeth on the fixed (47 vs. 62-70) and movable chelal fingers (47 vs. 62-65), by the carapace length (0.60 mm vs. 0.81-1.02 mm), by the pedipalpal length (2.90 mm vs. 4.49-5.33 mm), by the ratio of the pedipalpal femur length to breadth ratio (3.22 vs. 3.52-3.89), by the pedipalpal chelal length (1.00 mm vs. 1.64-1.94 mm), by the pedipalpal tibia length to breadth ratio (2.18 vs. 3.35-3.63), and by the body size (smaller vs. larger) (Table 1) (Ćurčić et al. 1996a).

From another epigean species from Montenegro *R. davor* new species, *R. hors* new species differs in many important respects: the form of the galea (lower vs. higher; Figs. 8, 29, and 30), in the cheliceral length of males (0.40-0.425 mm vs. 0.35 mm), in the pedipalpal length of males (3.52-3.64 mm vs. 2.90 mm), in the shape of the pedipalpal chelal palm (almost globular vs. ovate), in the pedipalpal femur length of males (0.70-0.71 mm vs. 0.58 mm), in the pedipalpal chelal length of males (1.30-1.31 mm vs. 1.00 mm), in the walking leg IV length of males (2.51 mm vs. 2.08 mm), and in the body size (larger vs. smaller) (Table 1).

#### *Roncus davor* new species

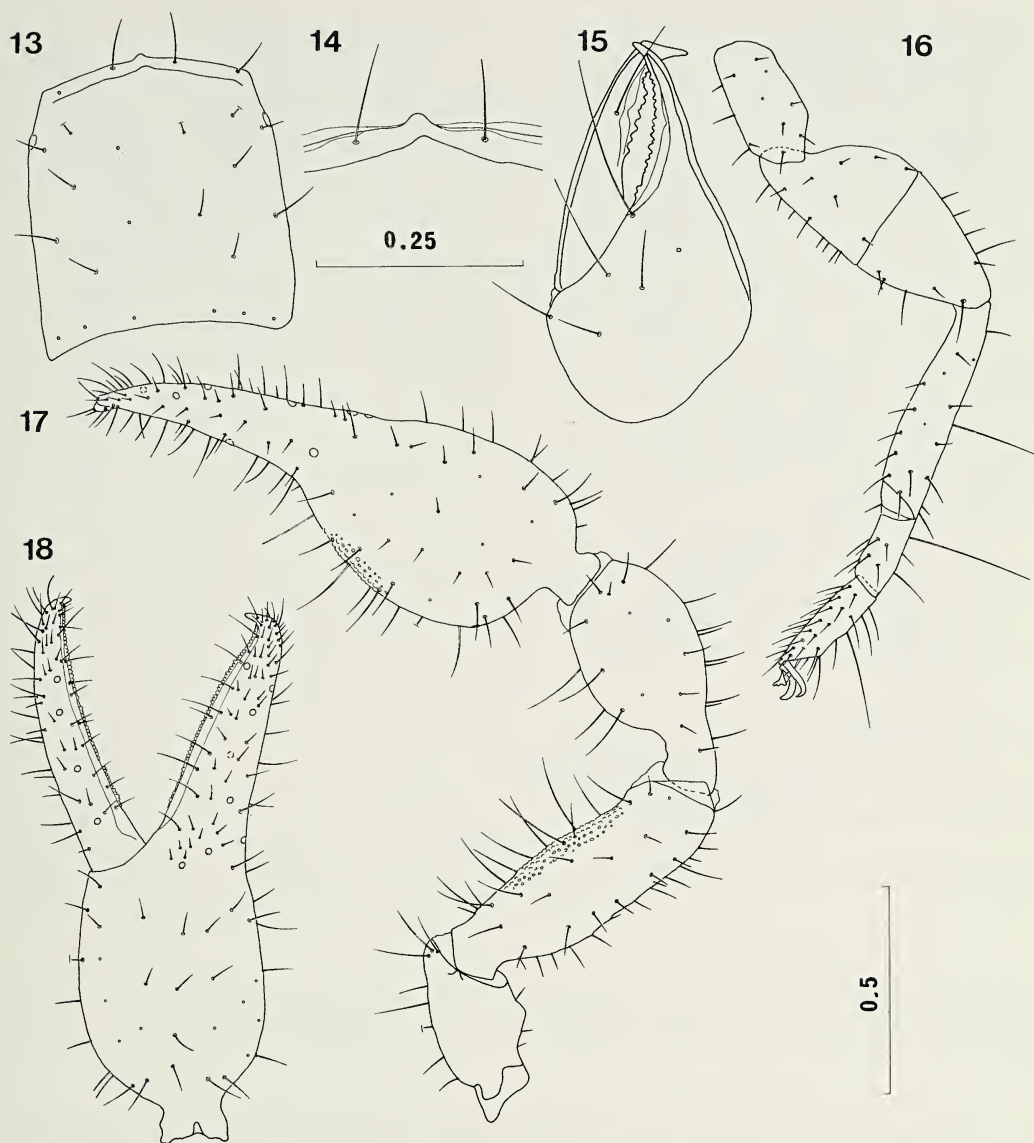
Figs. 13-25; Table 1

**Etymology.**—In Slav mythology, *Davor* is a chthonic deity, the son of Triglav (Petrović 1995).

**Specimens examined.**—Holotype female, and allotype male, from the canyon of the Sušica River, Mt. Durmitor (1100 m elev.), Montenegro, Yugoslavia, collected on 4 August 1992 by I.M. Karaman. Paratypes: 1♀, 1♂, 2 tritonymphs, and 1 deutonymph, from the village of Tepca, Mt. Durmitor (1000 m elev.), Montenegro, Yugoslavia, 5 August 1992, same collector (together with a specimen of *Neobisium* sp.).

**Description** (based on adults).—Epistome small and rounded, knob-like; (Fig. 14) or low and triangular (Fig. 20). A pair of small eyes (with flattened lenses) present (Figs. 13, 19).



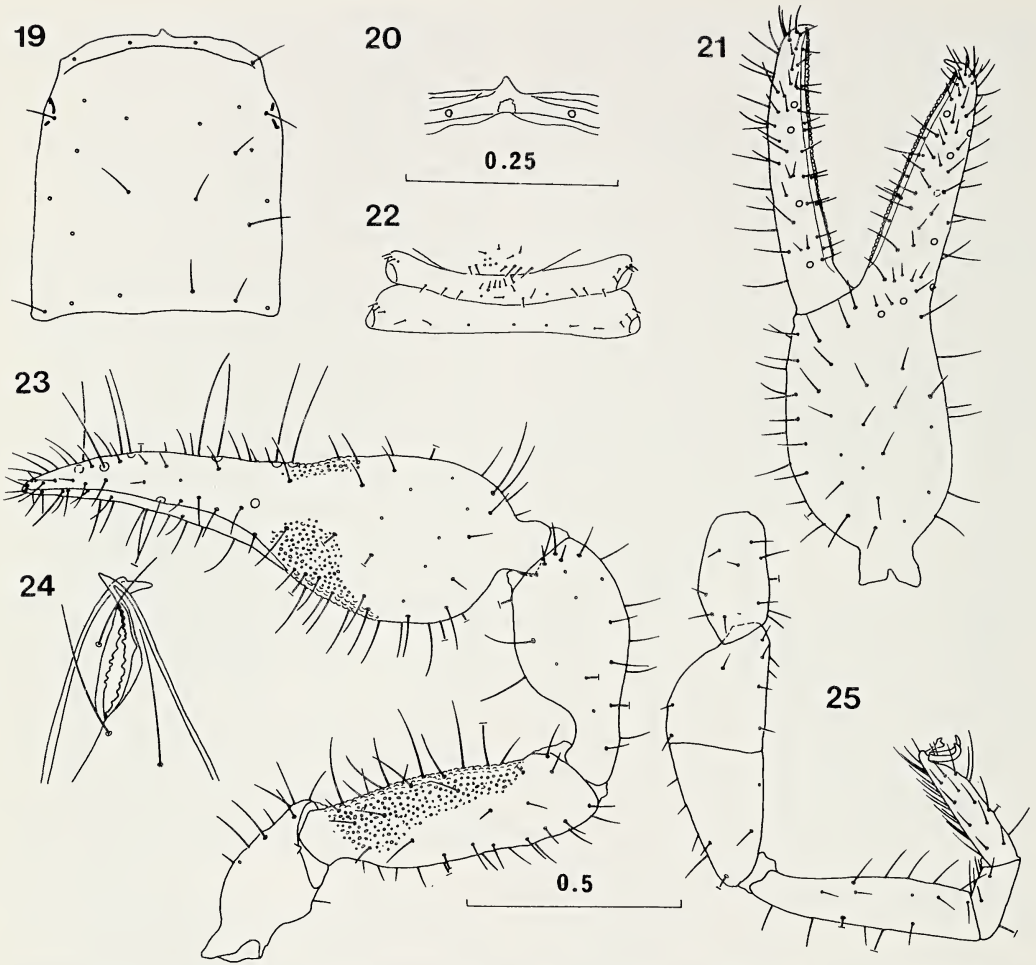


Figures 13–18.—*Roncus davor* new species, holotype female. 13, Carapace; 14, Epistome; 15, Chelicera; 16, Leg IV; 17, Right pedipalp (trichobothria omitted); 18, Pedipalpal chela (trichobothria omitted). Scales in mm.

Setal formulae:  $4+6+2+4+2+6 = 24$  (female) and  $4+6+2+4+2+6 = 24$  setae (male). Carapace reticulate throughout.

Tergites I–X with 6-9-11-12-11-11-12-12-11-9, 6-8-10-11-12-11-12-11-11-10 (females), and 6-8-10-11-10-11-11-10-9-9 setae (male). Abdominal tergites I–X and sternites V–X smooth, uniseriate, and entire. Female genital area: sternite II with 10–12 small setae, clustered into two groups on either side of the mid-line; sternite III with 10 or 11 posterior

setae and 3 or 4 suprastigmatic setae on either side; sternite IV with 11 or 12 marginal setae and 3 small setae along each stigma. Male genital area (Fig. 22): sternite II with 14–17 median and posterior setae (of these, 9 or 10 are retromarginal); sternite III with 4–7 (2+2 or 3+4) anterior, 10–12 posterior setae, and 3 or 4 suprastigmatic setae on either side; sternite IV with 7–10 posterior setae and 3 microsetae along each stigma. Sternites V–X with 14-13-15-15-14-12 and 14-15-13-14-



Figures 19–25.—*Roncus davor* new species, allotype male. 19, Carapace; 20, Epistome; 21, Pedipalpal chela (trichobothria omitted); 22, Genital area; 23, Pedipalp; 24, Cheliceral fingers; 26, Leg IV. Scale lines in mm.

15-14 (female) and 14-14-13-13-14-13 and 14-15-13-14-15-14 setae (male). Twelfth abdominal segment with two pairs of small setae.

Cheliceral spinneret (galea) small, low, and rounded (Figs. 15, 24). Cheliceral palm with six setae, movable finger with one seta. Flagellum eight-bladed (1 short proximal blade and seven longer blades distally), characteristic of the genus *Roncus*.

Apex of pedipalpal coxa with four long setae. Pedipalpal trochanter with a small tubercle, femur with a small exterolateral tubercle and interior granulations; patella (tibia) smooth; chelal palm either with interior (Fig. 17) or with both interior and exterior granulations (Fig. 23). Chelal palm ovate (dorsal

view). No microsetae proximal to trichobothria *eb* and *esb*; instead, 5–8 microsetae distal to *eb* and *esb* present (Figs. 18, 21). Fixed chelal finger with (male) 53–56 and (female) 55–57 teeth, movable chelal finger with 54–56 (male) and 55–57 teeth (female). Chelal fingers longer than chelal palm and distinctly shorter than pedipalpal femur (Table 1). Trichobothrial pattern: *ist* equidistant from *isb* and *est*; *sb* equidistant from *b* and *sr*; *st* closer to *t* than to *sb*. Distribution of trichobothria as illustrated in Figs. 19, 21.

Tibia IV, metatarsus IV and tarsus IV each with a long tactile seta (Fig. 25).

Morphometric ratios and linear measurements are presented in Table 1.

**Distribution.**—Montenegro, Yugoslavia;



epigean (in high elevation leaf-litter, soil, and humus). Probably endemic to the area.

**Diagnosis.**—From *R. yaginumai*, this new species is easily distinguished by the form of the pedipalpal articles (more elongate vs. less elongate; Figs. 17, 23) (Ćurčić et al. 1996a), by the relative position of the trichobothrium ist (closer to *est* than to *isb* vs. equidistant from *est* and *isb*), by the pedipalpal length of females (4.49–5.33 mm vs. 3.245–3.845 mm), by the pedipalpal chelal length to breadth ratio of females (3.35–3.63 vs. 2.83–2.89), by the pedipalpal chelal length of females (1.64–1.69 mm vs. 1.16–1.33 mm).

For comparison with *R. hors* new species see the 'Diagnosis' of that species.

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## RESEARCH NOTE

### ASSESSMENT OF THE RANDOM AMPLIFIED POLYMORPHIC DNA (RAPD) TECHNIQUE FOR THE ANALYSIS OF SPIDER POPULATIONS

The ability to determine the degree of genetic relatedness between different populations (both geographic and morphologic) of spiders would be of great value in many areas of spider biology. For example, it would allow the testing of the hypotheses that woodland fragments can act as habitat islands (Beaumont 1993) and that spiders can pass freely between real islands by aerial dispersal (Duffey 1956). It would also allow the investigation of the basis (genetic or environmental) of the intra-species size and shape variation seen in geographically separate populations of some species (e.g., Lycosidae: *Trochosa terricola* Thorell 1856 and *Pardosa pullata* (Clerck 1757) from widely separated peat-bog sites (Curtis & Stinglhammer 1986)).

Multi-locus DNA profiling ("finger-printing" Jeffreys et al. 1985a,b, 1991) experiments using the human DNA probes 33.6 and 33.15 (Jeffreys et al. 1985a, b) on genomic DNA of *P. pullata* had previously demonstrated that there were no sequences complementary to either of these probes in the genome of this lycosid (Beaumont 1993). For this reason, and also because spiders (particularly the smaller species) are so small that they might not contain sufficient DNA to generate a conventional DNA profile (5 µg; Bruford et al. 1992), a different approach to genetic analysis was adopted. The technique of random amplified polymorphic DNA (RAPD) analysis (Williams et al. 1990) or DNA amplification fingerprinting (DAF --Caetano-Anolles et al. 1991) has been successfully used in recent years to examine genetic relationships in a wide variety of species, including plants (Virk et al. 1995), insects (Hadrys et al. 1993), humans and other mammals (Welsh et al. 1991; Williams et al. 1990), and micro-organisms

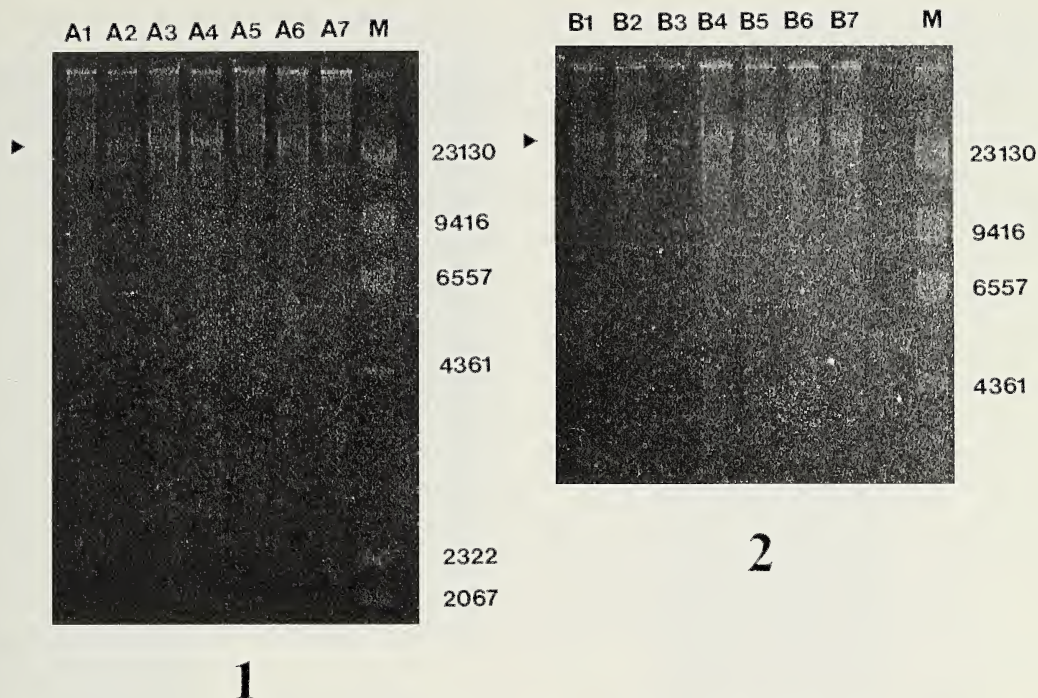
(Caetano-Anolles et al. 1991; Welsh & McClelland 1990). This technique uses an arbitrarily chosen oligonucleotide primer in a low stringency polymerase chain reaction (PCR --Saiki et al. 1988; Newton & Graham 1994) to generate a series of amplified products of different sizes from a target (usually intact genomic) DNA. These products are then separated by conventional agarose or polyacrylamide gel electrophoresis (Sambrook et al. 1990). The pattern of fragments produced is specific for the combination of primer and target DNA used (and the precise conditions of the PCR) and is attributed to the distribution of primer-complementary sequences within the target DNA. Since this is an amplification method, it can generate useful data from very small amounts of target DNA (e.g., as little as 1 ng; Hedrick 1992). Also, because of the ease of synthesis of primers and the speed of the PCR itself, it is feasible to screen large numbers of primers under different experimental conditions until a combination producing a suitable pattern of bands is found.

A preliminary investigation was thus undertaken to assess the suitability of the RAPD method for the genetic analysis of spider populations. The study used six different primers and genomic DNA isolated from siblings of two different broods of the theraphosid *Brachypelma albopilosa* (Valerio 1980). This spider was chosen because it was possible to purchase broods of known parentage. It was hoped to identify one or more primer(s) that would reliably enable both identification of siblings and discrimination between members of different broods.

#### METHODS

Two broods of juvenile (third instar) specimens of *B. albopilosa* of different parentage





Figures 1, 2.—Agarose gels (0.8%) showing intact, high molecular weight genomic DNA (▶) isolated from specimens of *Brachypelma albopilosa* from two different broods: 1, brood A; 2, brood B. 1–7 are different individuals within each brood. Each sample represents 10% of the total amount of DNA isolated from each specimen. M = marker DNA: genomic DNA of bacteriophage  $\lambda$  digested with the restriction enzyme *Hind*III. Sizes of the DNA fragments are indicated in base pairs (bp.). There is 0.5  $\mu$ g of DNA in the 23,130 bp. band. The amount of DNA in each sample of *Brachypelma albopilosa* DNA was estimated by comparison with the bands in the marker lane as recommended by Bruford et al. (1992).

were purchased from Ronald N. Baxter (Entomological Supplies), 45 Chudleigh Crescent, Ilford, Essex, IG3 9AT, England, UK. These were designated A and B, maintained under starvation conditions for four days after delivery (to ensure ablation of intestinal fauna) and then stored at  $-80^{\circ}\text{C}$ . Voucher material of these specimens has been deposited at the Paisley Natural History Museum, Paisley Museum & Art Galleries, High Street, Paisley, PA1 2BA, Scotland, UK. DNA was extracted from these whole, frozen, individual spiders using a protocol based on a procedure for the isolation of intact, high molecular weight DNA from mammalian cells described by Sambrook et al. (1990) and described in full elsewhere (Beaumont 1993). After extraction, an aliquot of each DNA sample was run on an agarose gel to assess concentration, purity and integrity.

Six oligonucleotide primers were synthe-

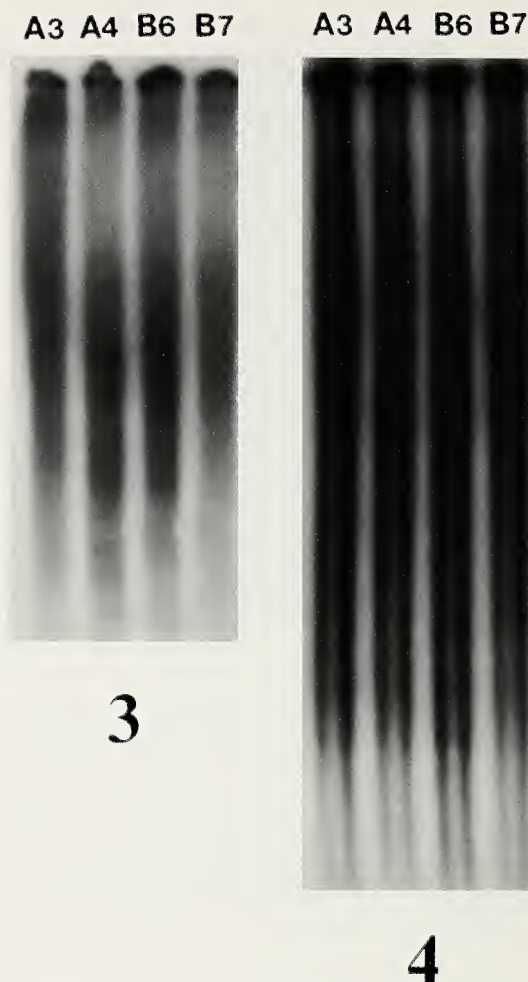
sized for use in these experiments. Some of the sequences were chosen because of their usefulness in previous RAPD experiments (e.g., 1 & 4 by Caetano-Anolles et al. 1991); others were selected as they had been successfully used as probes in conventional DNA profiling experiments (2 & 3 by Weising et al. 1989; 2 by Debarro et al. 1994); still others were wholly arbitrary (5 & 6). The sequences of these primers (shown 5'–3' from left to right) are as follows: primer 1: CGCGCCGG, primer 2: GATAGATAGATAGATA, primer 3: GACAGACAGACAGACA, primer 4: GTGATCGCAG, primer 5: GTAAAACGACGCCAGT, primer 6: CTAGGTCTTGAAAGGAGTGC.

Polymerase chain reactions, using 16 ng of *B. albopilosa* genomic DNA as target, were performed as described (Welsh et al. 1991), except that the annealing temperatures were kept constant throughout all the

cycles of any one reaction. Two sets of reactions were carried out for each primer, the first with an annealing temperature of 40 °C, the second with an annealing temperature of 30 °C. Agarose and polyacrylamide gels were run as described in Tris-borate electrophoresis (TBE) buffer (Sambrook et al. 1990). Agarose gels (0.8%) were used to assess the concentration, purity and integrity of intact genomic DNA; 5% polyacrylamide gels ( $\pm$  7M urea) were used to resolve the products of the PCR reactions. If appropriate, gels were stained in a solution of ethidium bromide ( $0.5 \mu\text{gml}^{-1}$  in TBE) for 15–30 min. Polyacrylamide gels were dried under vacuum at 80 °C (2 h), wrapped in plastic film ("Saran-Wrap", Dow Chemical Co.) and any bands visualized by exposure of the gel to autoradiography film ("Hyperfilm-MP", Amersham, UK) in an autoradiography cassette fitted with two intensifying screens for 1–4 days at –80 °C.

### RESULTS AND DISCUSSION

Intact, high molecular weight genomic DNA was successfully and consistently isolated from *B. albopilosa* (Figs. 1, 2). The amount of DNA isolated from each spider was estimated to be 0.25–1.0  $\mu\text{g}$ , sufficient for many RAPD analyses to be performed on each individual. In other studies, intact, high molecular weight genomic DNA was successfully isolated from other spider species (Amaurobiidae: *Amaurobius similis* (Blackwall 1845); Linyphiidae: *Leptyphantus leprosus* (Ohlert 1865); Lycosidae: *Pardosa pullata*; Araneidae: *Zygiella x-notata* (Clerck 1757)) by the same method (not shown). The genomic DNAs from two individuals from each brood (3 & 4 from A, 6 & 7 from B) were used in polymerase chain reactions with each of the six primers (separately). The reaction products were separated by polyacrylamide gel electrophoresis, the gels dried and the DNA fragments visualized by autoradiography. The results of these reactions are summarized in Tables 1–6, and examples of the banding patterns produced are shown in Figs. 3–6. It should be noted that the DNA fragments on several gels were also visualized by ethidium bromide staining before drying (not shown) and a comparison of the stained gel and autoradiograph showed that no additional bands

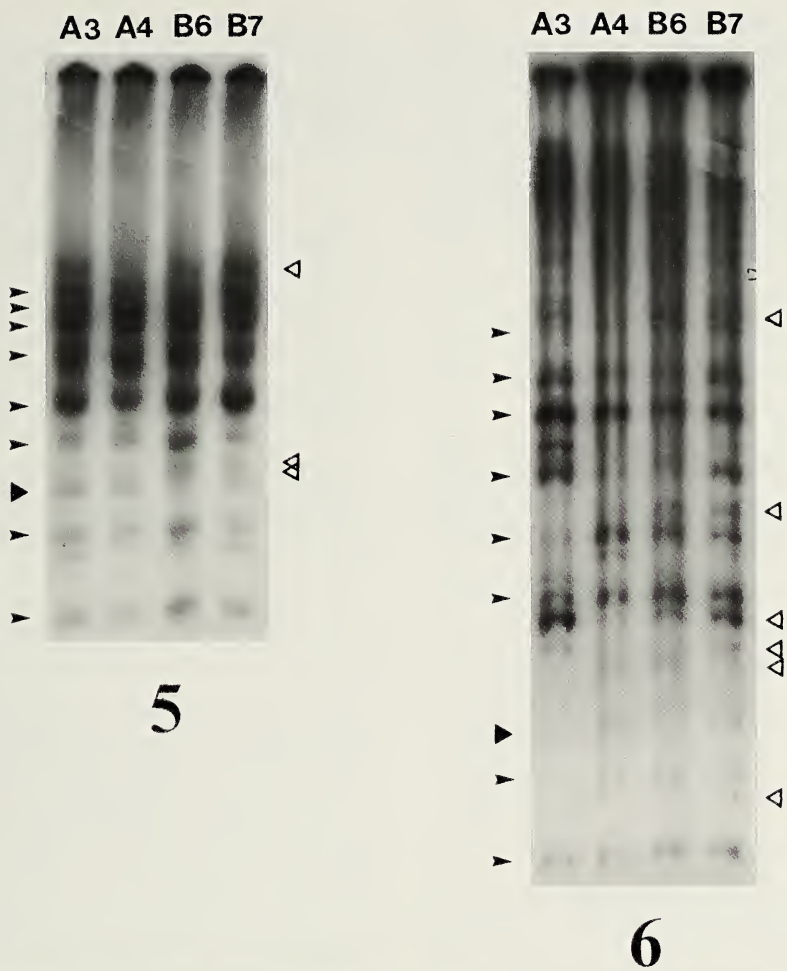


Figures 3, 4.—Autoradiographs showing the results of RAPD analysis on individuals A3, A4, B6 and B7 using primer 3 with a PCR annealing temperature of: 3, 40°C; 4, 30 °C.

were detected by autoradiography. Thus, it is unnecessary to use radio-labelled nucleotides in the RAPD procedure, thus simplifying this process.

The only primer that consistently failed to produce amplified products of discrete sizes was primer 3 (Figs. 3, 4). At both annealing temperatures, this primer generated many fragments of similar sizes that were not resolved by the electrophoretic technique used, resulting in the appearance of long smears on the autoradiographs. This suggests that there are many binding sites complementary to this primer throughout the tar-





Figures 5, 6.—Autoradiographs showing the results of RAPD analysis on individuals A3, A4, B6 and B7 using primer 4 with a PCR annealing temperature of: 5, 40 °C; 6, 30 °C. Products common to all four samples (►), or to A3 and A4 only (►), or to B6 and B7 only (◄) are indicated.

get DNA. It is possible that this primer is annealing to microsatellite loci and that annealing is occurring at many overlapping sites. For all the other primers used, products of discrete sizes (different in both num-

ber and size for each primer) were consistently produced. This suggests there are smaller numbers of complementary sites available to which these primers can anneal. The exact pattern produced by a primer var-

Table 1.—Total number of DNA fragments generated by PCR amplification from each target DNA at each annealing temperature by primers 1, 2, 4–6.

DNA	Primer 1		Primer 2		Primer 4		Primer 5		Primer 6	
	30 °C	40 °C	30 °C	40 °C	30 °C	40 °C	30 °C	40 °C	30 °C	40 °C
A3	2	5	5	2	15	11	5	9	8	7
A4	4	5	6	6	11	9	8	9	5	6
B6	8	5	7	8	15	11	6	13	5	6
B7	7	3	5	7	16	12	4	11	5	4

Table 2.—Number of common amplified DNA fragments generated from target DNAs A3 and A4 at each annealing temperature by primers 1, 2, 4–6.

Primer	Annealing temperature	
	30 °C	40 °C
1	2	3
2	5	0
4	9	9
5	5	9
6	2	6

Table 3.—Numbers of common amplified DNA fragments expressed as percentages of total number of DNA fragments generated from target DNAs A3 and (A4) at each annealing temperature by primers 1, 2, 4–6.

Primer	Annealing temperature	
	30 °C	40 °C
1	100 (50)	60 (60)
2	100 (83)	0 (0)
4	60 (82)	82 (100)
5	100 (63)	100 (100)
6	25 (40)	86 (100)

ied according to the annealing temperature used during the PCR. Primer 4 provides good examples of the type of pattern produced (Figs. 5, 6). At both annealing temperatures, this primer generated many amplified products from each target DNA and the patterns of products observed were very similar from all four target DNAs. Due to these similarities, reliable differentiation between inter- and intra-family relationships was not possible using this primer. And, in-

Table 4.—Number of common amplified DNA fragments generated from target DNAs B6 and B7 at each annealing temperature by primers 1, 2, 4–6.

Primer	Annealing temperature	
	30 °C	40 °C
1	4	3
2	4	4
4	14	11
5	4	10
6	5	4

Table 5.—Numbers of common amplified DNA fragments expressed as percentages of total number of DNA fragments generated from target DNAs B6 and (B7) at each annealing temperature by primers 1, 2, 4–6.

Primer	Annealing temperature	
	30 °C	40 °C
1	50 (57)	60 (100)
2	57 (80)	50 (57)
4	93 (88)	100 (92)
5	67 (100)	77 (91)
6	100 (100)	67 (100)

deed, for this same reason, none of the primers used could reliably differentiate between these types of relationships (see Tables 1–6).

Although no primer was found that could allow both identification of siblings and discrimination between members of different broods, the feasibility of the procedure was established. Analysis of the organization and sequence of the *B. albopilosa* genome, particularly of any repetitive sequences that may be found, should permit the design of more useful primers. It should be noted, however, that there are known to be some problems associated with RAPD analysis. For example, and as in all DNA profiling analyses, it can be difficult to determine whether similar bands in different lanes are matching or not. Also, distinguishing heterozygotes from homozygotes and establishing Mendelian patterns of inheritance may prove problematic. Finally, there can be problems of data reproducibility between experiments. Some of these problems, and methods that might be employed to over-

Table 6.—Numbers of common amplified DNA fragments generated at each annealing temperature from target DNAs A3, A4, B6 and B7 by primers 1, 2, 4–6.

Primer	Annealing temperature	
	30 °C	40 °C
1	0	3
2	3	0
4	8	8
5	4	6
6	2	3



come them, are discussed by Williams et al. (1990) and Hedrick (1992).

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 33, 34, *A-us y-us*, male. Scale = 1.0 mm.

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# The Journal of ARACHNOLOGY

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Cover: Female *Araneus pima* wrapping prey. Taken with Nikon FM2 and 105mm Macro lens with manual flash, Fuji velvia film. Photo by Bryan Reynolds of Albuquerque, New Mexico.

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Publication date: 29 December 1997



## RE-DESCRIPTION OF *TOGWOTEEUS BICEPS* (ARACHNIDA, OPILIONES, SCLEROSOMATIDAE) WITH NOTES ON ITS MORPHOLOGY, KARYOLOGY AND PHENOLOGY

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**ABSTRACT.** The harvestman genus *Togwoteeus* Roewer 1952 is monotypic. Its only species, *T. biceps* (Thorell 1877), is known from throughout western Canada and USA and is newly recorded from California, Nebraska, Nevada, Oregon, South Dakota, and Utah. This species occurs below 500 m and at the highest elevation (4100 m) of any recorded harvestman in North America. It ranges from about 33–54° N and exhibits considerable variation in its morphological measurements. Twenty-seven such measurements are summarized for 80 males and 74 females. Ultrastructural details of the integument, appendages and genital organs are presented. The karyotype is  $2n = 22$  for both sexes. All chromosomes are metacentric and obvious sex chromosomes were not detected. Immature *T. biceps* overwinter and reach adulthood in late spring or early summer. Adults die by late fall.

Members of the monotypic genus *Togwoteeus* Roewer 1952 are common harvestmen of prairie and mountain habitats in western regions of Canada and USA. For nearly 100 years, the single species currently recognized was known by the name *Homolophus biceps* (Thorell 1877). Cokendolpher (1987) proposed the new combination *Togwoteeus biceps* because true members of the genus *Homolophus* Banks 1894 are known only from Asia. *Togwoteeus* was transferred from the family Phalangidae to the Sclerosomatidae by Crawford (1992). Examination of museum specimens revealed considerable variation within this species, e.g., specimens from British Columbia and Idaho had exceptionally longer legs. Because this species is found over such a large region of North America and was poorly studied, we sought to determine if the observed morphological variations were due to the existence of unrecognized new species. While doing this study we documented morphological, chromosomal, and phenological information which we herein present.

### METHODS

Collections from which samples were examined, other than those of the authors, are

listed in the Acknowledgments. Specimens used for measurements are described in Table 1. Those from Edmonton and Writing-on-Stone are retained by RGH. Those from Wyoming and Utah are in the American Museum of Natural History. One count and 27 measurements were made: four of the body, eight of the pedipalp, femora I–IV, tibiae I–IV, three of the genital operculum, four of the ocular tubercle; and the number of metatarsal bands on leg II. Measurements, examination methods, and terminology were as presented by Cokendolpher (1981), except the palpal femur and tibia lengths were measured along their greatest lengths (i.e., in lateral view, longitudinal distance between diagonal lines drawn from basoventral point to proximodistal point, Fig. 36, *fl* and *tl*). The ovipositors were cleared with lactophenol for examination and drawing of the seminal receptacles. Statistics were analyzed with the statistical computer program SPSS<sup>®</sup>. For morphological measurements two-tailed *t*-tests were used. For the single count, the Kolmogorov-Smirnov two-sample test was used. Alcohol preserved specimens were critical point dried, sputter coated with gold and photographed with scanning electron microscopes (SEM). Photographs

<sup>1</sup>To whom correspondence should be addressed.

Table 1.—Specimens used for body measurements.

Location	Latitude N, Longitude W	Altitude (m)	Collection dates	Males	Females
Edmonton, Alberta	53°46', 113°25'	580	May–August 1982	20	20
Writing-on-Stone Provincial Park, Alberta	49°05', 111°38'	915	May–July 1981	20	20
Grand Teton National Park, Wyoming	43°29', 110°50'	2260–2440	July–August 1962, August 1969	20	14
Timpanogos, Utah County & Mill Creek Canyon, Salt Lake County, Utah	40°26–41', 111°30–50'	1585–1725	May–June 1931–1941	20	20

were also taken through dissecting microscopes. Methods for the preparation of the karyotypes are reported by Cokendolpher & Brown (1985). The karyotypes were done in July 1983 from gonads of subadult specimens collected at the Logan Canyon summit, Cache County, Utah. The specimens were collected under rocks in the snow and transported alive in an ice-chest to Lubbock, Texas. They were maintained in the refrigerator until dissected.

RESULTS AND DISCUSSION

*Togwoteeus* Roewer

*Mitopus*: Thorell 1877:525; Banks 1893:206.  
*Homolophus*: Banks 1894:160, 163, 164 (in part); 1900:123; 1901:674; Cockerell 1911:253; Roewer 1910:259 (in part); 1912:31 (in part); 1923:879–880 (in part); 1929:2 (in part); 1952:268 (in part); 1957:355 (in part); 1960:24, 30 (in part); Comstock 1912:66, 71; 1940:66, 71; Kästner 1937:392 (in part); Katayama & Post 1974:13–14; Cokendolpher & Cokendolpher 1982:1215; Cokendolpher 1985:371, 399 (in part); 1987:89, 94 (in part).  
*Togwoteus* Roewer 1952:268; 1957:356; Crawford 1992:45; Cokendolpher & Lee 1993:16.

**Type species.**—*Togwoteus granipalpus* Roewer 1952; by monotypy. Junior subjective synonym of *Mitopus biceps* Thorell 1877 and *Homolophus punctatus* Banks 1894.

**Diagnosis.**—Body with thick, hard, tuberculate-microgranulate cuticle; off-center micropores present on dorsal tubercles; preocular area without mound but with two groups of small denticles near anterior margin edge; supracheliceral lamellae well developed and toothed; pedipalps without apophyses on distal ends of patellae or tibiae in juveniles or adults, without campaniform organ on distal end of femora, claw smooth, not toothed; male

pedipalps enlarged, tarsus bulbous at base and with ventral teeth; legs generally short, femur I usually equal to or shorter than body length, no pseudoarticular nodules in femora; leg coxae without lateral rows of denticles; penis alate, i.e., with wing-like extensions.

**Comparisons.**—The presence of an alate penis and a smooth palpal claw separate *Togwoteus* from all sclerosomatid opilions, except *Leuronychus* Banks 1900 and *Cosmobunus* Simon 1879. These genera can be easily distinguished from *Togwoteus* by their longer legs (femur I always much longer than the body length) and lack of denticles in front of the ocular tubercle.

**Subordinate taxa.**—The genus is monotypic.

**Distribution.**—Western North America (Fig. 1).

*Togwoteus biceps* (Thorell)  
(Figs. 1–38)

*Mitopus biceps* Thorell 1877:525–528; Pavesi 1889:531; Banks 1893:206, 207; Cokendolpher 1987:94; Crawford 1992:45.  
*Homolophus biceps*: Banks 1894:163; 1895:431; 1900:123; 1901:674; 1902:593; 1916:72; Cockerell 1907:620; 1911:253; Roewer 1912:31; 1923:880; 1957:355; Comstock 1912:71; 1940:71; Levi & Levi 1951:219, 221, fig. 1; 1955:32; 1968:245; Goodnight & Goodnight 1953:175; Holmberg 1970:127–129, figs. 3, 4, 3, 7, A, 1; Schmoller 1970:127–128, 132; 1971a:323, 327; 1971b:346, 348; Bragg & Leech 1972:67; Katayama & Post 1974:8–10, 13, 14, 20, fig. 1; Holmberg et al. 1981:19; Holmberg & Kokko 1983:49–52, figs. 1–4; Cokendolpher 1985:399; 1987:94; Poinar 1985:122.  
*Togwoteus biceps*: Cokendolpher 1987:94; Cokendolpher 1993:129, 132, 138; Cokendolpher & Lee 1993:16, 25–31.



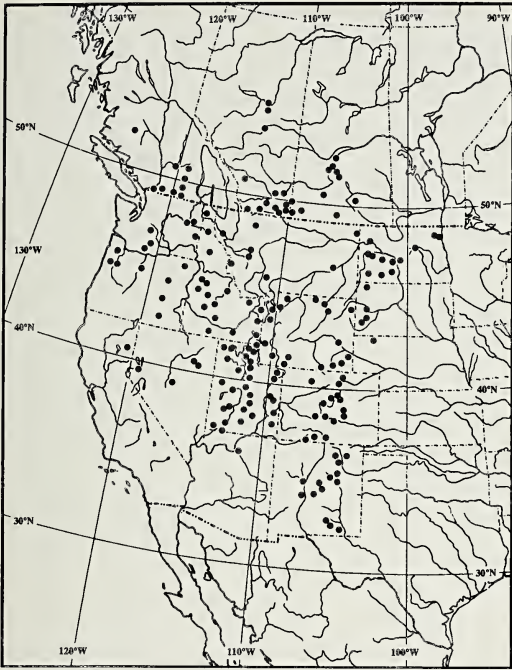


Figure 1.—Distribution of *Togwoteus biceps* in western North America. Collection sites that had nearly the same location were not mapped.

*Togwoteus* (= *Homolophus*) *biceps*: Edgar 1990: 567.

*Homolophus punctatus* Banks 1894:164; 1901:674; Roewer 1923:880–881; Cokendolpher 1987:94.

*Togwoteus granipalpus* Roewer 1952:268, fig. 2; 1957:356; Levi & Levi 1955:32; Cokendolpher 1985:399; 1987:94; Crawford 1992:45.

*Globipes* sp.: Blake 1945:232 (misidentification).

**Types.**—The holotype of *Togwoteus granipalpus* is labeled “Dr. E.C. Zimmerman 18.8.1951 Opiliones. Leptobuninae No. 14 *Togwoteus granipalpus* Rwr 1M Genotypus n.g. n.sp. Wyoming. Togwotee Pass 2743 m, Teton Co., Zimmerman Leh Rwr det. 1952” and is housed in Senckenberg Natur-Museum (RII/11047/14). JCC examined the specimen and found it to be a female.

The types of *Mitopus biceps* were from USA: Idaho, no specific locality (5 July), and Colorado, [Clear Creek County] Gray’s Peak (a little below the summit), (7 July). These were apparently lost by the early part of the 20th century (Roewer 1923). Dr. Arbocco (pers. comm. 1981) checked the collection at Museo Civico di Storia Naturale “Giacoma Doria” twice for the types of this species without success and agreed that the lectotype

should be designated from material collected by Thorell at the Naturhistoriska Riksmuseet. Thus, we are designating the male and female from the Naturhistoriska Riksmuseet as the lectotype and paralectotype, respectively. They have both been labeled as such: “det. Cokendolpher 1981”. The original data labels in the vial with the types correspond with those published except for the date: “Riksmuseets Entomologiska Afdelnig. Collectio T. Thorell *Mitopus biceps* Thor. Idaho U.S.A. (Packard) no. 73”, “March 2 1891”, and “*Mitopus biceps* Thor. Idaho U.S.A. Packard Md.” As the labels are of unknown authorship it is possible they are incorrect. The specimens closely match Thorell’s (1877) detailed written description.

The types of *Homolophus punctatus* were from the USA: Olympia, Thurston County, Washington (1♂, Trevor Kincaid) and Bear, Adams County, Idaho (1♀, L.M. Cockerell). These have apparently been lost. They were not examined by Roewer (1923).

**Distribution.**—Three most western provinces of Canada and 14 western states of USA (Fig. 1). The records for California, Nebraska, Nevada, Oregon, South Dakota, and Utah are the first published for these states.

The female (SMF RII/2663/5) reported by Roewer (1957) from Pueblo, México, is either misidentified or mislabeled. The specimen cannot be located at Senckenberg Natur-Museum (Grasshoff pers. comm. 1981), and possibly originated from Pueblo, New Mexico, or the well-known Pueblo, Colorado.

We are unable to locate the specimens reported from near Centennial, Wyoming by Blake (1945) as *Globipes* sp. They are certainly misidentified, as no known *Globipes* sp. occurs in or near Wyoming, the nearest records being from Arizona and New Mexico (JCC pers. obs.). Blake’s specimens are probably members of *Togwoteus*, as this is the only genus of the region which resembles *Globipes*. We have also examined a series of *T. biceps* collected in Medicine Bow Mountains, near Blake’s collection site.

**Records.**—(Based only on specimens examined; including adults and some immatures.) **CANADA.** *Alberta*: Athabasca; 30 km N of Athabasca; Big Hill Springs Provincial Park, near Cochrane; Etzikomi; Lodgepole Pine Campground area, Cypress Hills Provincial Park; Edmonton; Elkwater; Hwy. 48, N Elkwater Provincial Park; Etzikom; Leth-



bridge; 16 km S Magrath; Medicine Hat; Seven Persons; Canadian Forces Base, Suffield; Waterton Lakes; Chief Mountain Road, Waterton Lakes National Park; Lewis Overthrust, Waterton Lakes National Park; Lookout Butte, Waterton Lakes National Park; Writing-on-Stone Provincial Park. *British Columbia*: Anarchist Mountain; Apex Mountain, near Keremeos; near Inkaneeep Park along Okanogan River; Kamloops; Kleena Kleene; Manning Provincial Park; Beaver Pond Trail, Manning Provincial Park; isolated small park 6.4 km N Oliver; Meyers Flats, Oliver; Vaseaux Lake, Oliver; Ecological Reserve, Osoyoos; Kruger Springs, Osoyoos; Osoyoos Lake; Salmon Arm; Summerland; Rattlesnake Point, Vernon; White Lake, 10 km S of Penticton. *Saskatchewan*: Buffalo Pound Provincial Park; Central Block and West Block, Cypress Hills Provincial Park; 17.7 km S Cypress Hills Provincial Park; Cypress Lake; 9.7 km WSW Dundurn; Fort Walsh; Killdeer badlands; Saskatoon; Beaver Creek Park, 12.9 km SSW Saskatoon; 4.8 km NE Saskatoon; 8 km S Saskatoon; 20.9 km N Saskatoon; 22.5 km SSW Saskatoon; Saskatchewan Landing; Saskatchewan Landing Provincial Park. *USA. Arizona*: Coconino County: Kaibab National Forest, Grand Canyon. *California*: Lassen County: Blue Lake. *Colorado*: County?: Mummy Range (3353 m); Pingree Park. Archuleta County: Pagosa Springs. Boulder County: Arapaho Pass; Boulder Cañon (2246 m); Longs Peak Valley, Rocky Mountain National Park (2774 m); Longs Peak, Rocky Mountain National Park (3400 and 4100 m). Chaffee County: Upper Spring Creek, near Monarch Pass. Clear Creek County: Loveland Pass; Mt. Evans; Summit Lake, Mt. Evans (3900 m). Conejos County: at top of Cumbres Pass; Trujillo Meadow Camp, 4.8 km N Cumbres (3048 m). Custer County: West Cliff (= Westcliffe). El Paso County: on mountain side above Hwy 70, Pikes Peak; Pikes Peak (3048, 3658, 4115m); Canyon, Pikes Peak; Printing Office, Pikes Peak (3048 m). Fremont County: Wet Mountains, Stations 40, 47, 50 and 52 (2316, 2164, 2072, and 2127 m). Gilpin County: Gilpin. Grand County: Arapaho Peak (3962 m); Milner Pass. Gunnison County: Meyers Gulch. La Plata County: Cascade; Eldora (2438 m); Electra Lake (2560 m); Ward (2743 m). Larimer County: Glen Haven; near Long's Park campground south of Estes Park Village; 16.1 km W Estes Park, Rocky Mountain National Park; Big Thompson Canyon, 11.3 km S Estes Park; Rustic. Pitkin County: Aspen (3292 m). Rio Blanco County: small run beside route 13 ca. 9.7 km S Axial. Saguache County: Cochetopa Pass; Rist Cañon, Fort Collins. Summit County: Hoosier Pass, south of Breckenridge. Teller County: near Florissant. *Idaho*: Adams County: Summit, 11.3 km NE Council; canyon east of Meadows; north end of Payette Lake. Bear Lake County: Brentwood Lodge, Fish Haven; George-

town; Montpelier. Boise County: 12.9 km S Galena (=Gardena?) Summit, junction Cherry and Coyote Creeks; Boise River, near entrance of north fork; Boundary Creek, Boise National Forest. Bonner County: Hana Flats, 8 km SW Nordman. Bonneville County: 16.1 km S Swan Valley. Cassia County: Rock Creek Canyon, 24 km S of Rock Creek; Sublett Reservoir. Clark County: Spencer. Custer County: Salmon River Gorge, above Challis. Fremont County: St. Anthony. Kootenai County: Coeur d'Alene. Lincoln County: Little Wood River, Pagari. Nez Perce County: 8 km NW Culdesac. Twin Falls County: no specific location. Washington County: 11.3 km NE Cambridge. *Montana*: Carbon County: E Rosebud (1890 m); Medicine Lake. Gallatin County: 9.7 km W Belgrade, W Gallatin River. Glacier County: 7 km W Browning. Granite County: Clark Fork near Bearmouth; Nimrod. Ravalli County: Gird's Creek, Hamilton. Sanders County: Thompson Falls. *Nebraska*: Dawes County: Belmont. *Nevada*: Elko County: Thomas Canyon Camp, 14.5 km SSE Lamoille Ruby Mountains (2286 m); Ruby Valley. Lander County: Kingston Camp, 48.3 km S Austin, Toiyabe Range. Washoe County: Reno. *New Mexico*: Bernalillo County: Sandia Mountains; near Crest, Sandia Mountains. Los Alamos County: Camp May (2900 m). Otero County: Bluff Springs, 14.5 km S Cloudcroft; Camp Deerhead, 1.6 km S Cloudcroft; Lincoln National Forest, Fir Forest Campground. San Miguel County: Gallinas Canyon, NW of Las Vegas; just W Cowles; Lake Kathrine Trail, Cowles; Penitente Park, Cowles; Spirit Lake Trail, Cowles. Sandoval County: Jemez Mountains; Sandia Mountains. Santa Fe County: Lake Peak NE of Santa Fe; near ski area NE Santa Fe. Taos County: 4.8 km E Questa; Frazier Mt., Twining; Williams Lake Trail, Twining; Gold Hill near Red River; just E of Rio Pueblo; Red River Pass; trail from Red River to Wheeler Peak. Valencia County: Grants, Mt. Taylor Summit (3353 m); Mount Taylor. *North Dakota*: Benson County: no specific location. Billings County: T.R. National Memorial Park. Dunn County: T146-R97-S25-P400; Killdeer Mountains. McKenzie County: N unit T.R. Park; T146-R98-S16-P110. Mclean County: Washburn Park; 6.4 km S Washburn Rest Area. Mercer County: Hazen. Monton County: no specific location. Pembina County: no specific location. Slope County: Chalky Buttes; T136-R102-S14-P200; Burning Coal Vein. Williams County: no specific location. *Oregon*: Benton County: Corvallis Entomological Research Farm; Marys Peak Parker Creek, near Marys Peak Campground. Grant County: Malheur National Forest, Blue Mountain Hot Springs. Harney County: 24 km S Burns; Steen Mountains. Jefferson County: head of Metolius River, Riverside Forest Camp. Union County: Insler, Harris Mountains. Yamhill County: McMinnville. *South Dakota*:

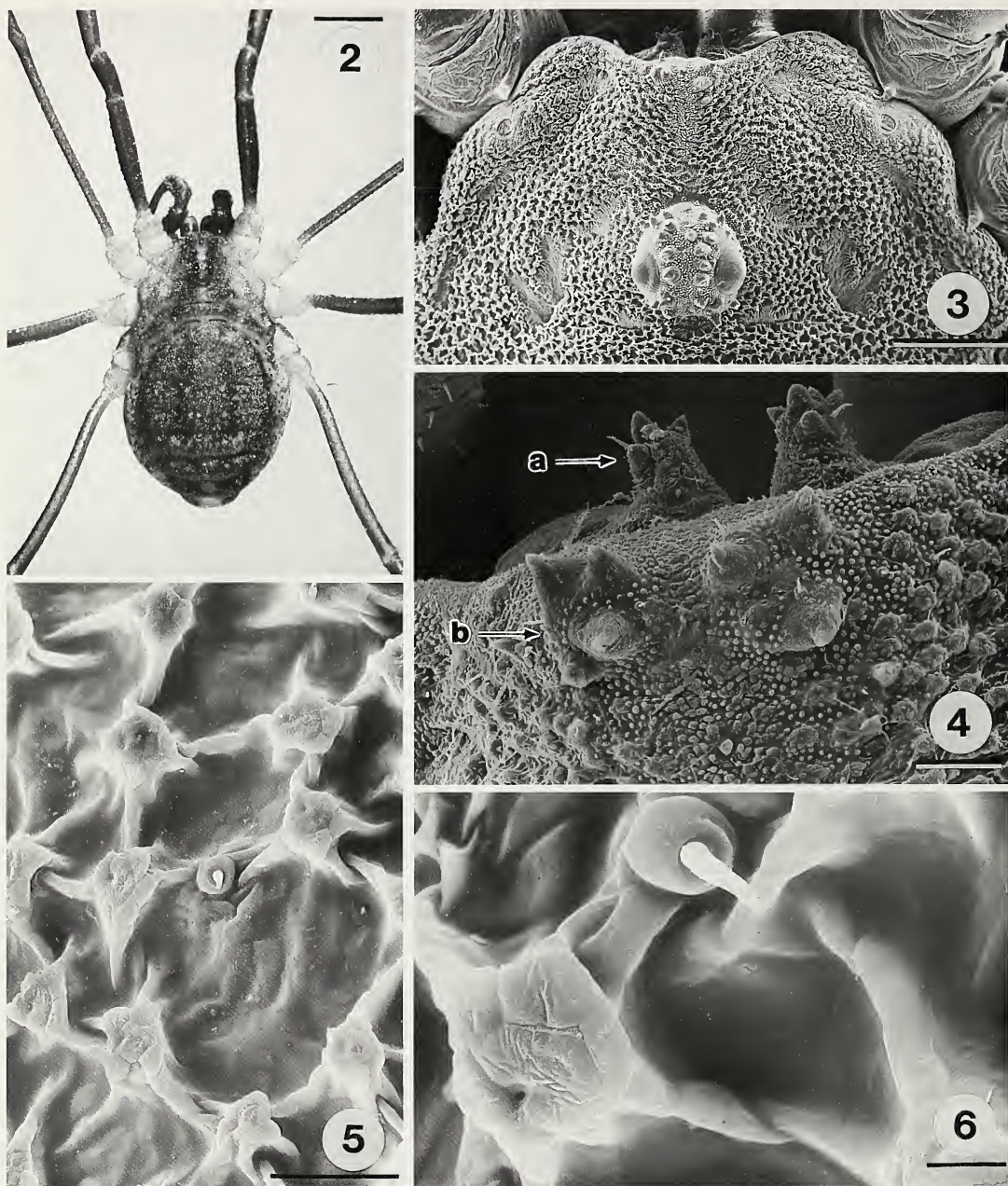


Custer County: Custer State Park. Lawrence County: Custer Park; 5.5 km S Deadwood on Highway 85A; Spring Creek Camp, 17.7 km NE Hill City. Pennington County: Mount Rushmore. *Utah*: County?: Blacksmith Fork Canyon; Butterfield Canyon, Oquirrh Mountains; Othess Mantes Canyon; Puffer Lake. Beaver County: Beaver Canyon, 16 km (direction?) from Beaver City; Kents Lake Camp, 25.8 km E Beaver City. Box Elder County: Bear River City; Clear Creek, Raft River Mountains; Dove Creek, Raft River Mountains; Rabbit Springs, 9.7 km N Lucin; Raft River Mountains, 12.9 km S Lynn. Cache County: Beaver Mountain, Wasatch Range; Logan Canyon; Logan River; Red Banks, Logan Canyon (1829 m). Dagget County: Hideout Canyon; Junction Deep and Carter Creek. Emery County: Ferron Reservoir; Huntington Canyon. Garfield or Wayne County: Horse Valley, Henry Mountains. Garfield County: Aquarius Plateau, Steep Creek; Blue Spruce Camp, 29 km N Escalante (2438 m); Wild Cat Ranger Station, 24.2 km N Boulder. Grand County: La Sal Mountains; Mirror Lake, Uintah Mountains; Warner Ranger Station, 45.1 km ESE Moar (2804 m). Iron County: Cedar Breaks. Juab County: Trout Creek. Morgan County: Bells Canyon. Millard County: Oak Creek Camp, 14 km E Oak City. Rich County: Bear Lake (east side). Salt Lake County: 6.4 km up City Creek Canyon, Salt Lake City; City Creek, Salt Lake City; Emigration Canyon; Mill Creek Canyon; Mill Creek, Salt Lake City; Salt Lake City. San Juan County: Buckboard Flat Camp, 11.3 km W Monticello (2682 m); Dalton Springs Camp, 8 km W Monticello (2591 m); La Sal Mountains. Sanpete County: Moroni. Sevier County: Fish Lake. Summit County: Beaver Canyon; Hoop Lake, Uintah Mountains. Tooele County: Loop Camp, 20.9 km SW Grantsville (2256 m); South Willow Canyon. Uintah County: Iron Springs Camp, 40.3 km N Vernal (2652 m); Kaler Hollow Camp, 35.4 km NNW Vernal (2713 m). Utah County: American Fork Canyon, Timponogos; Aspen Grove; Timpanogos. Wasatch County: Provo River at North Fork. Washington County: Pine Valley Mountains; Zion National Park. *Washington*: Kittitas County: Ellensburg. Klickitat County: near Maryhill, 11.3 km E Daller Ferry; Trout Lake County Park. Stevens County: 4.8 km N, 12.8 km NE and 40 km N Wellpinit. Whitman County: Elberton. *Wyoming*: County?: Freemouth. Albany County: Medicine Bow Peak, near Centennial; Woods Landing. Big Horn County: Porcupine Camp, 53.7 km E Lovell. Carbon County: Bottle Creek Camp, 11.3 km SW of Encampment; 12.9 km SW of Encampment (2621 m). Converse County: Medicine Bow Mountains; Summit Laramie Mountains near Pole Mountains. Crook County: Reuter Canyon Camp, 8 km NW Sundance (1737 m); 8 km N Sundance. Johnson County: Bighorn National Forest, Circle

Park Rec. Area. Laramie County: Cheyenne. Lincoln County: Cokeville. Park County: Lake Creek Camp, 20.9 km SE Cooke; Lost Creek Camp; Mount Washburn Summit, Yellowstone National Park. Sheridan County: Ranger Creek Camp, 30.6 km SW Big Horn (2377 m). Sublette County: Lower Green River Lake, Wind River Range (2438 m). Sweetwater County: Green River. Teton County: Grand Teton National Park; near Moran; Moran Junction; Owl Creek Headquarters, 48 km N Jackson; Stewart River Station; spring runs crossing Route 287 in Togwotee Pass; Teton Pass; Wilson; Old Faithful, Yellowstone National Park; near Yellowstone Lake, Yellowstone National Park.

**Description.**—Body with thick, hard, tuberculate-microgranulate cuticle on dorsal surface (Figs. 2, 3); off-center micropores present on dorsal tubercles (Figs. 5, 6); base coloration varies from amber to black, with dorsal specks or patterns of lighter color sometimes present; dorsum sometimes with faint central figure; males tend to be more sclerotized and have more denticles and therefore appear darker than females; preocular area without mound but with two groups of small denticles near anterior margin edge (Fig. 4, arrow b); supracheliceral lamellae well developed and toothed (Fig. 4, arrow a); ocular tubercle low, rounded, covered by many prominent spines (Fig. 3); darker ring often encircling each eye; light area extends between the eyes and from the ocular tubercle to the anterior edge of the prosoma and usually forms a distinct bifid stripe (Fig. 2). Abdomen with faint indication of segmentation dorsally. Genital operculum without noticeable crest ventrally; with many microscopic spicules dorsally (Figs. 7–9). Chelicerae not enlarged, without apophyses on jaws, ventral spur on basal segment large and covered with many spicules; with 4–6 slit sensilla on second segment (Figs. 18, 21). Pedipalps without apophyses on distal ends of patellae or tibiae in juveniles or adults, distal end of femora without campaniform organ (slit-sensillum present), claw smooth, not toothed (Figs. 13, 14, 17); pedipalps sexually dimorphic; male pedipalps modified, enlarged, tarsus bulbous at base and with two rows of ventral denticles; midventral area of tibia slightly compressed (most noticeable on mesal side) (Figs. 14–16, 36, 37). Legs generally short and wide; femur I as wide or wider than ocular tubercle, femora I usually equal to or shorter than body length, no pseudoarticular nodules in femora,



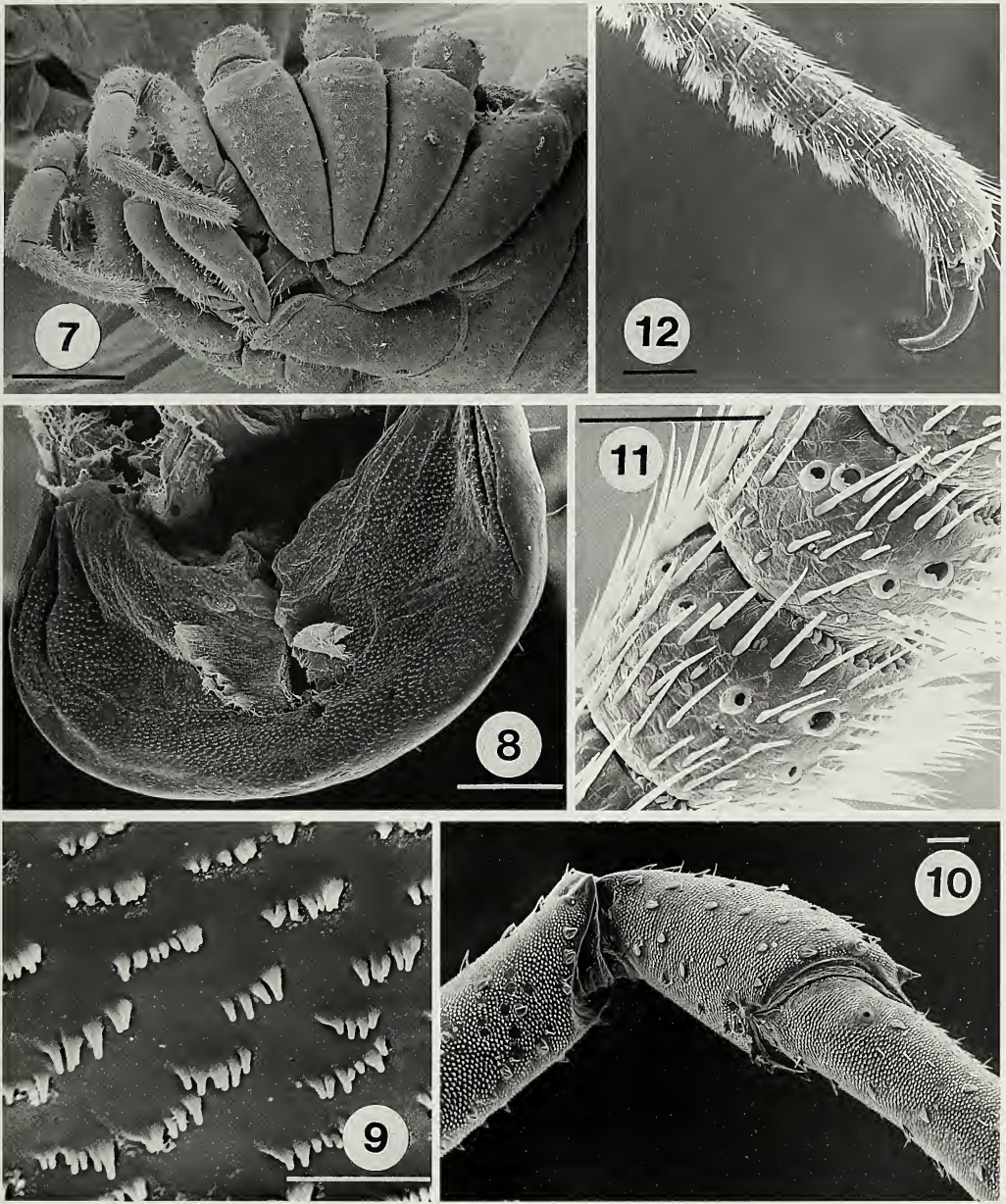


Figures 2–6.—Body and integument of *Togwoteeus biceps*. 2, Dorsal view of adult male (non-SEM); 3, Ocular tubercle and anterior portion of cephalothorax of male; 4, Supracheliceral lamella (arrow a) and anterior portion of cephalothorax of female with tubercles (arrow b); 5, Cuticle of prosoma of male; 6, Detail of cuticle. Scales = 0.5 mm in Figs. 2, 3; 0.1 mm in Fig. 4; 0.05 mm in Fig. 5; 10  $\mu$ m in Fig. 6.

tibiae II with (longer legged specimens) or without (lectotype and shorter legged specimens) pseudosegments; tibiae I, III, IV without pseudosegments; femora, patellae, tibiae with randomly spaced (without rows) pointed tubercles (Fig. 10); patellae and distal tips of

leg femora and tibiae often darkly shaded; each leg coxa with center spine dorsally, with at most a weakly developed lateral row of denticles (Fig. 7). Penis alate (Figs. 22–25, 31–33); ca. 5  $\mu$ m longitudinal slit near the tip of the stylus of the penis glans (Fig. 24). Ovi-



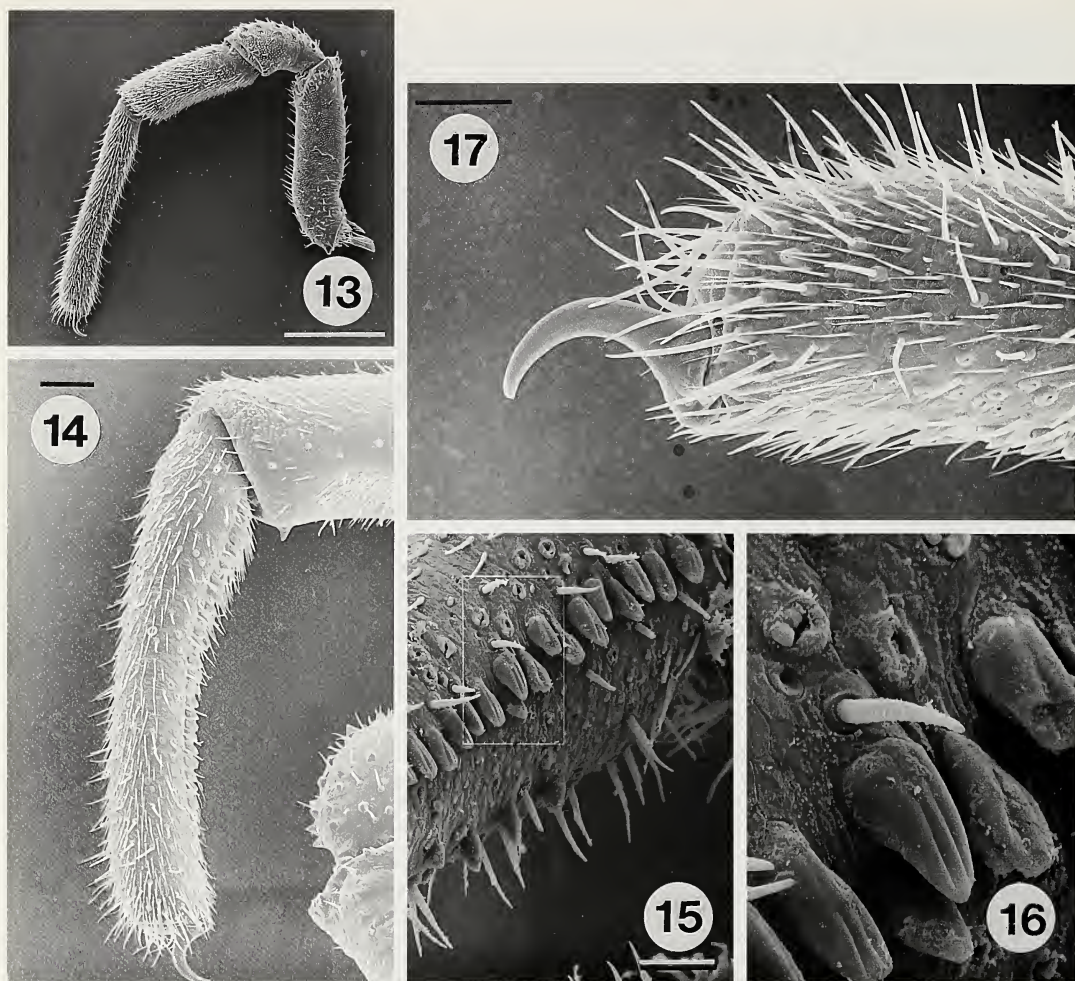


Figures 7–12.—Morphology and anatomy of *Togwoteeus biceps*. 7, Anteroventral view of anterior portion of male; 8, Spicules on inner lining of the anterior edge of male genital operculum; 9, Detail of operculum spicules; 10, Lateral view of leg I of female; 11, Detail of tarsal leg pores of female; 12, Tip of leg tarsus with smooth claw of male. Scales = 1 mm in Fig. 7; 0.1 mm in Figs. 8, 10, 12; 0.5 mm in Fig. 11; 10  $\mu$ m in Fig. 9.

positor relatively long, 34 segmented in paralectotype; with four slit-sensilla (two dorsal, two ventral) per lateral half; 3 segmented furca (Figs. 26, 27, 35). Ovipositor enclosed in two sheaths, details as in Figs. 28–30. Seminal receptacles as in Fig. 34, located in segments 3–4 of ovipositor (Fig. 35).

**Body measurements.**—The results of measuring 80 males and 74 females are given in Table 2. No simple measurement cline was observed between the four areas (Table 1) and the data were pooled. Female body measurements are larger than those of males. Male pedipalps measurements are larger than fe-





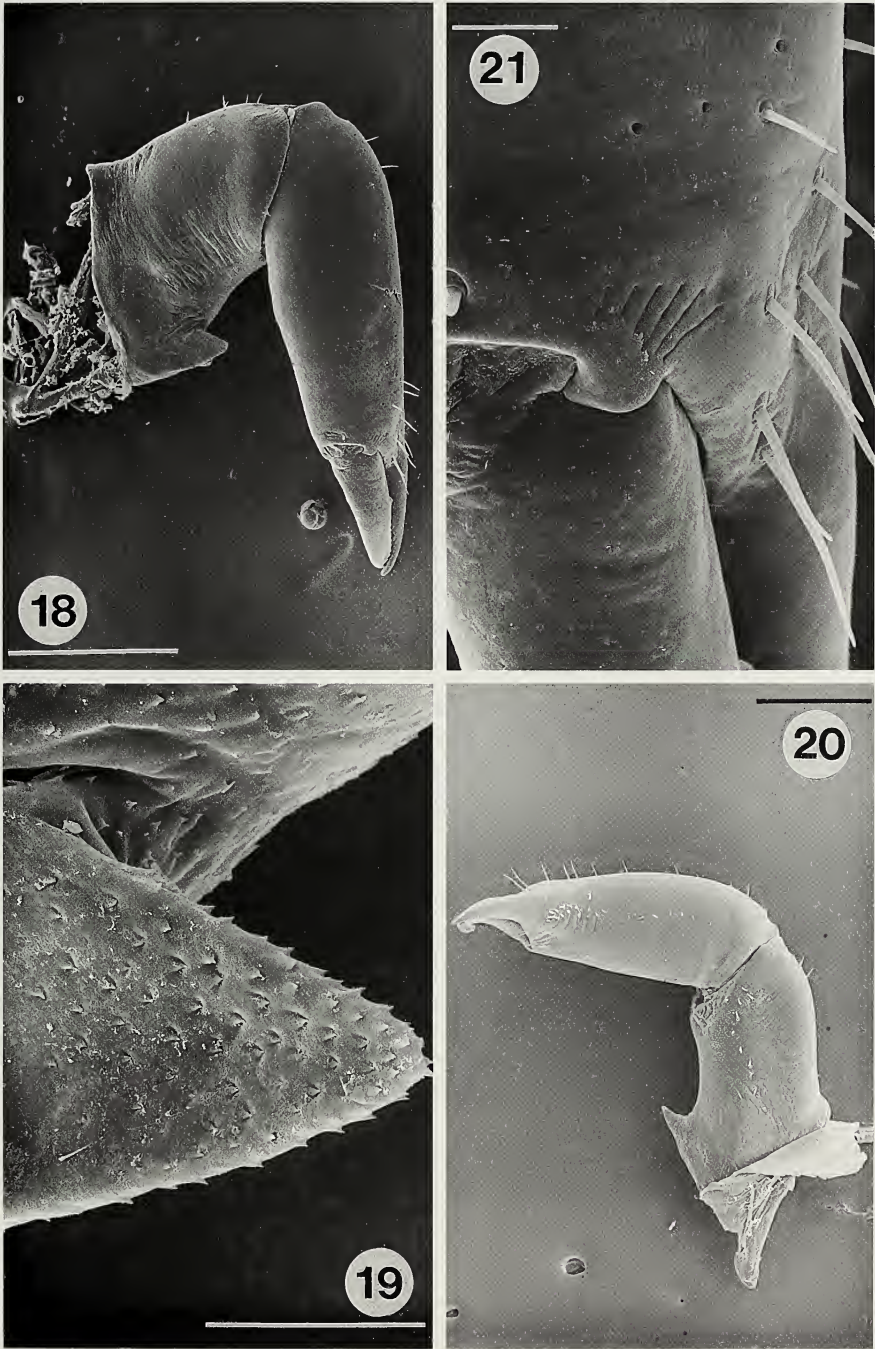
Figures 13–17.—Right pedipalp of *Togwoteeus biceps*. 13, Lateral view of female; 14, Detail of male tarsus; 15, Denticles and pores on tarsus of male; 16, Detail (3.4× enlargement) from insert in Fig. 15; 17, Smooth claw of male. Scales = 0.5 mm in Fig. 13; 0.1 mm in Fig. 14; 0.05 mm in Figure 17; 50  $\mu$ m in Fig. 15.

males, except for palpal tarsus length (which is longer in females) and width (which is the same for both sexes). Male leg measurements were generally longer except for femur II and IV. The length of the genital operculum is longer in males but wider at the base in females. The neck width is the same. Male and female measurements for the ocular tubercle are the same except that the female's is slightly closer to the anterior margin. The mode numbers of metatarsal bands for both sexes are four; the range varies between 2–10.

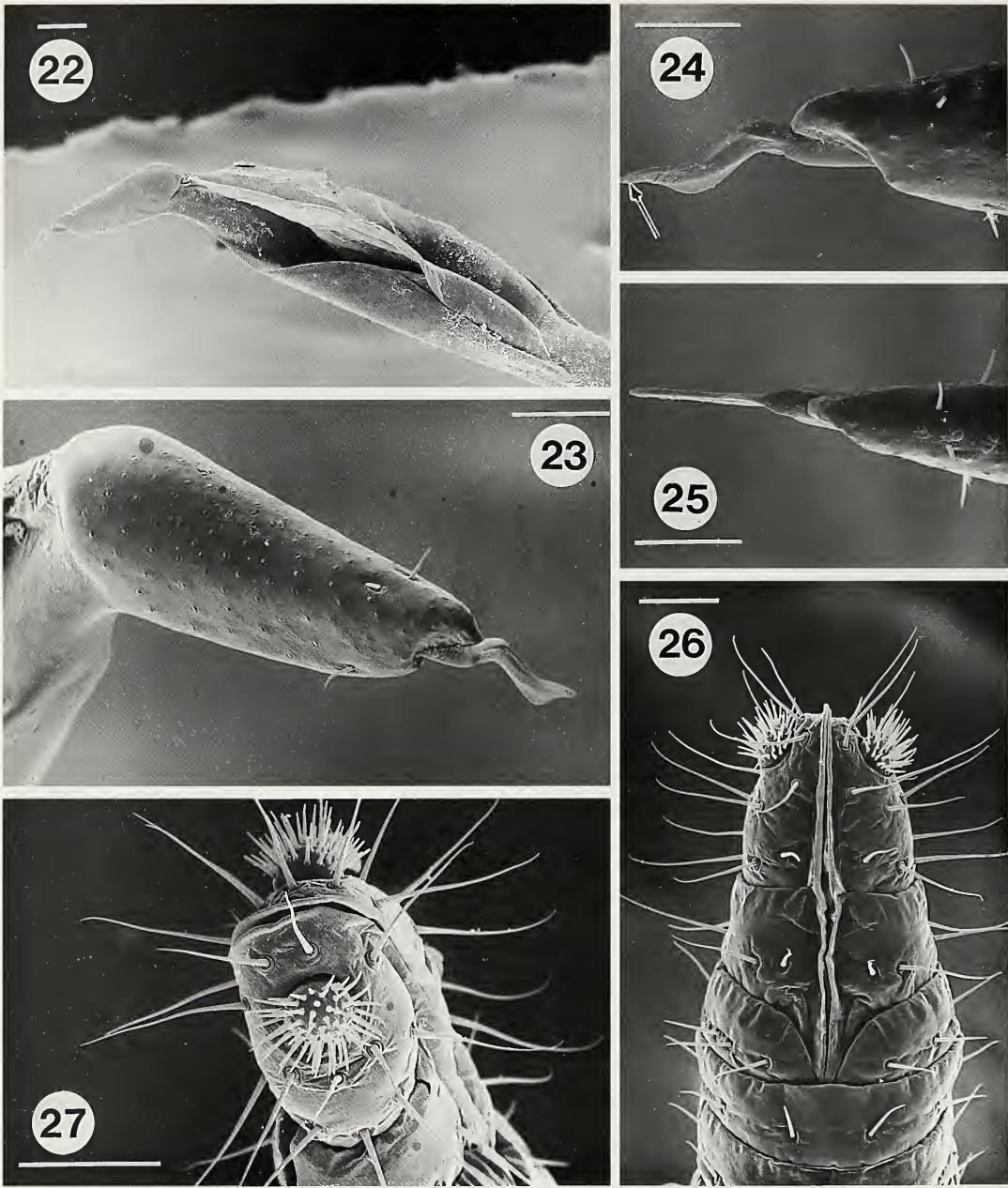
**Ultrastructure.**—The pedipalp sense organs of *Togwoteeus* appear similar to those observed by Spicer (1987) in other harvestmen, i.e., *Leiobunum* C. Koch 1839 and *Eu-*

*mesosoma* Cokendolpher 1980. Like Spicer, we found sensilla trichodea and chaetica on the pedipalps of *T. biceps* (Figs. 11, 12, 14, 17). The “tarsal organs” of Spicer were also observed on the ventral surface of the pedipalp tarsus (Figs. 15, 16). The prosomal dorsum revealed a tuberculate-microgranulate morphology (Figs. 3–4). The prominent tubercles have asymmetrical arms, with the central regions containing off-center micropores. The abdominal setae arise from tubercles elevated from the surface of the integument. These tubercles appear to be constricted at their bases. The dorsal morphology of *T. biceps* is unlike any other harvestman thus far examined (cf. Murphree 1988). The off-center





Figures 18–21.—Chelicerae of female *Togwoteus biceps*. 18, Lateral view; 19, Lateral view of basal tooth with numerous spicules (close-up of Fig. 18); 20, Mesal view; 21, Detail of slit sense organ at base of movable cheliceral jaw (close-up of Fig. 18). Scales = 0.5 mm in Figs. 18, 20; 0.05 mm in Figs. 19, 21.



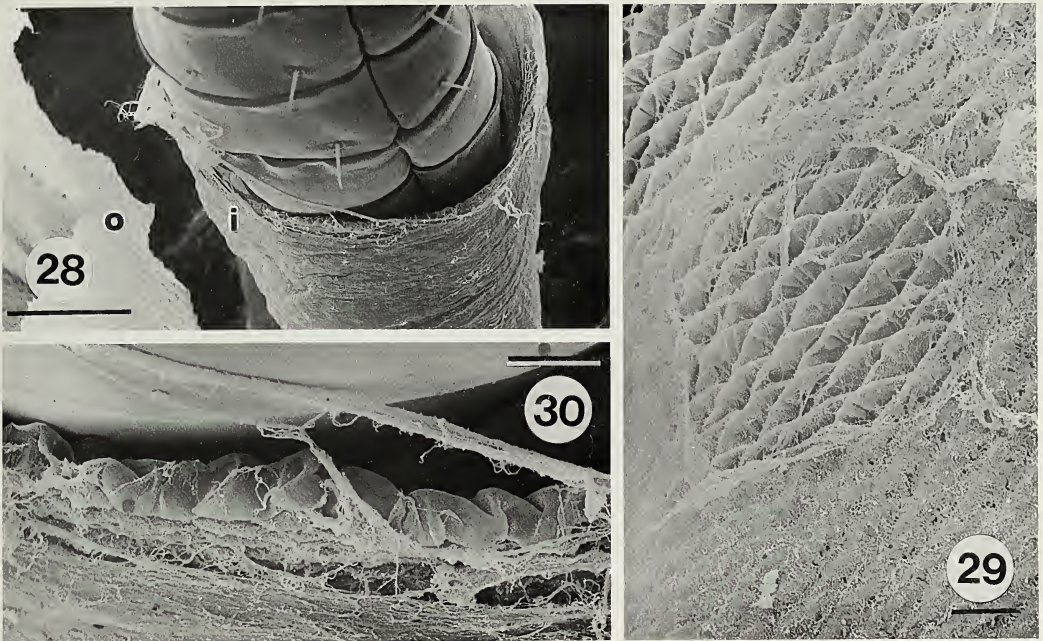
Figures 22–27.—Genital structures of *Togwoteeus biceps*. 22, Ventrolateral view of distal end of penis; 23, Lateral view of glans of penis; 24, Lateral view of stylus of penis – arrow indicates location of a 5  $\mu$ m slit; 25, Dorsal view of stylus of penis; 26, Distal end of ovipositor with 3-segmented furca; 27, Distolateral view of sensillae on ovipositor. Scales = 0.1 mm in Figs. 22, 26, 27; 0.05 mm in Figs. 23–25.

placement of micropores is unlike the central placement of members of *Leiobunum* and *Hadrobunus* Banks 1900. *Eumesosoma* apparently does not have micropores atop of dorsal tubercles (Murphree 1988: Fig. 18). The ul-

trastructure of the ovipositor sheaths are herein illustrated for the first time as are some details of the penis and ovipositor.

**Variation.**—We occasionally found specimens that had leg lengths nearly double the





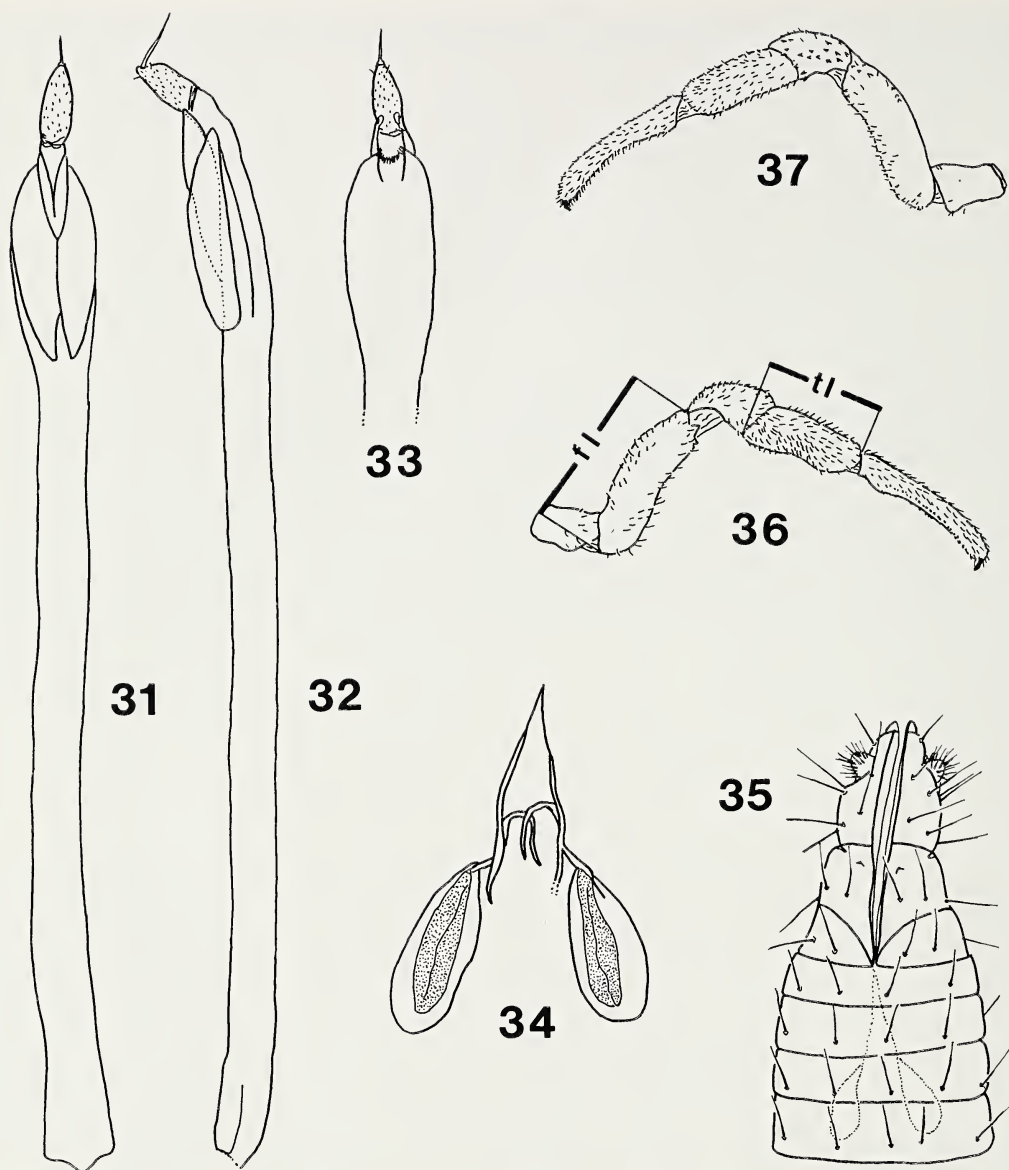
Figures 28–30.—Ovipositor of *Togwoteeus biceps*. 28, Mid-section of ovipositor and broken sheaths, o = outer and i = inner sheaths; 29, Expanded view of inner sheath of ovipositor; 30, Expanded view of cross-section of inner sheath. Scales = 0.1 mm in Fig. 28, 10  $\mu$ m in Figs. 29, 30.

normal. For example, a female specimen from near Osoyoos, British Columbia had a femur II length of 9.60 mm (cf. mean of 5.35 mm, Table 2). However after examining other characteristics and measuring many individuals, we concluded that these were exceptional individuals and not another species. Goodnight & Goodnight (1953) stated that a north-south cline in coloration could be demonstrated for this species. The lighter colored individuals were in the north and the darker colored individuals were in the south. While this may be partially true, it is not as simple as that. It appears age and sex of the animal may play a significant role in the color of the animal. Examination of series collected through time revealed older animals and males are darker. The role of elevation and moisture have not been investigated, but as evidenced in other arthropods they may play a role in the determination of pigmentation. There was no obvious cline in the morphological measurements of the specimens examined in this study.

**Anomalies.**—Holmberg & Kokko (1983) reported on an eye-less *T. biceps*. It had no ocular tubercle and only degenerate optic

nerve masses. This anomaly was found in only one specimen. During this study some abnormalities were noticed in the formation of the denticles near the anterior edge of the cephalothorax and the suprachelical lamellae. Usually one such structure was smaller than normal and with fewer and smaller denticles.

**Chromosomes.**—Karyotypes from two subadult males and one subadult female revealed  $2n = 22$ , all being metacentric chromosomes (Fig 38). Sex chromosomes were not detected in the male karyotypes. The chromosomes in the two karyotypes from the female were not condensed and sex chromosomes could not be distinguished. Studies detailing chromosomes of harvestmen are few. The known counts/karyotypes were presented or reviewed by Tsurusaki & Cokendolpher (1990) and Cokendolpher & Jones (1991). Including the present study, karyotypes of 40 species of the superfamily Phalangioidea are known. The diploid chromosome numbers thus far known for the superfamily range between 10 and 36, with 22 being recorded in several unrelated genera of the Protolophidae (*Protolophus* Banks 1893)



Figures 31–37.—Anatomy of *Togwoteeus biceps* (male lectotype, female paralectotype). 31, Ventral view of penis; 32, Lateral view of penis; 33, Dorsal view of distal end of penis; 34, Seminal receptacles; 35, Distal end of ovipositor with seminal receptacles (dotted lines); 36, Mesal view of male pedipalp; 37, Lateral view of male pedipalp. *fl* = femur length, *tl* = tibia length.

and Sclerosomatidae (*Dalquestia* Cokendolpher 1984, *Eumesosoma*, *Gagrellula* Roewer 1911, *Leiobunum*).

**Habitat.**—This species is found in many habitats. In the mountains specimens are often found in densely wooded areas as well as on windswept mountain-tops above the tree line. They also occur in many dry habitats, but often near water bodies, especially in northern

prairies. In the southern part of their range, they are restricted to higher elevations. They have been found under rocks, logs, and other ground debris. A few individuals were also obtained in deserted buildings. Only rarely have they been obtained by sweeping vegetation. They do not appear to aggregate in protected sites like many other sclerosomatids.

**Phenology.**—Although the collection data



Table 2.—Morphological measurements (mm) and counts of *Togwoteus biceps*. Data pooled from specimens described in Table 1. SE = Standard error. ns = not significant, probability > 0.05. Statistically significant larger values in bold.

Body part	Males			Females			<i>P</i>
	Mean (SE)	Range	<i>n</i>	Mean (SE)	Range	<i>n</i>	
<i>Body</i>							
Prosoma width	2.68 (0.031)	2.08–3.12	80	<b>2.87</b> (0.035)	2.04–3.40	74	<0.001
Body length	4.84 (0.053)	3.60–5.76	80	<b>6.16</b> (0.084)	3.72–7.48	74	<0.001
Abdomen width	2.89 (0.036)	1.88–3.08	80	<b>3.58</b> (0.049)	2.28–4.92	74	<0.001
Abdomen height	2.51 (0.029)	1.88–3.08	80	<b>3.40</b> (0.061)	1.88–4.68	74	<0.001
<i>Pedipalps</i>							
Femur length	<b>1.15</b> (0.015)	0.90–1.36	80	0.99 (0.013)	0.72–1.20	74	<0.001
Femur width	<b>0.33</b> (0.005)	0.24–0.44	80	0.25 (0.003)	0.16–0.30	74	<0.001
Patella length	<b>0.58</b> (0.006)	0.44–0.66	80	0.48 (0.006)	0.36–0.58	74	<0.001
Patella width	<b>0.35</b> (0.004)	0.26–0.40	80	0.30 (0.003)	0.22–0.36	74	<0.001
Tibia length	<b>0.81</b> (0.010)	0.62–1.00	80	0.70 (0.009)	0.48–0.88	74	<0.001
Tibia width	<b>0.34</b> (0.004)	0.24–0.44	80	0.26 (0.003)	0.20–0.34	74	<0.001
Tarsus length	1.06 (0.013)	0.82–1.28	80	<b>1.12</b> (0.014)	0.82–1.38	74	0.002
Tarsus width	0.17 (0.004)	0.12–0.24	80	0.17 (0.003)	0.10–0.22	74	0.23 ns
<i>Legs</i>							
Femur I length	<b>3.22</b> (0.087)	2.08–4.92	79	2.90 (0.072)	1.76–4.56	74	<0.006
Tibia I length	<b>2.59</b> (0.066)	1.60–3.84	78	2.28 (0.051)	1.52–3.40	73	<0.001
Femur II length	5.76 (0.174)	3.64–9.44	80	5.35 (0.156)	3.36–8.52	74	>0.08 ns
Tibia II length	<b>5.08</b> (0.156)	3.08–8.16	80	4.16 (0.130)	2.88–7.32	74	0.02
Femur III length	<b>3.45</b> (0.089)	2.24–5.20	80	3.13 (0.072)	2.04–4.56	74	0.006
Tibia III length	<b>2.71</b> (0.068)	1.72–3.80	80	2.42 (0.053)	1.60–3.56	74	0.001
Femur IV length	5.11 (0.137)	3.40–7.76	79	4.86 (0.116)	3.20–7.60	74	>0.16 ns
Tibia IV length	<b>3.80</b> (0.095)	2.52–5.60	77	3.49 (0.080)	2.32–5.40	74	0.015
<i>Genital operculum</i>							
Length	<b>3.13</b> (0.037)	2.48–3.80	80	2.92 (0.036)	2.16–3.48	74	<0.01
Neck width	1.28 (0.013)	0.99–1.52	80	1.29 (0.015)	0.96–1.52	74	0.56 ns
Base width	2.25 (0.026)	1.72–2.88	80	<b>2.39</b> (0.026)	1.76–2.92	74	<0.001
<i>Ocular tubercle</i>							
To anterior margin	<b>0.52</b> (0.007)	0.38–0.64	80	0.49 (0.007)	0.36–0.64	74	<0.004
Length	0.45 (0.004)	0.38–0.54	80	0.45 (0.006)	0.36–0.56	74	0.66 ns
Width	0.43 (0.003)	0.38–0.50	80	0.43 (0.004)	0.34–0.50	74	0.36 ns
Height	0.26 (0.005)	0.16–0.32	80	0.26 (0.004)	0.20–0.32	74	0.62 ns
<i>Metatarsal II bands</i>	4.82 (0.146)	2–8		4.53 (0.183)	2–10	73	0.35 ns

(Table 3) are biased (i.e., most collection dates in the summer, most specimens collected were larger — usually adults, most collection sites between 40–50°N latitude), it appears that *T. biceps* overwinters as immatures which become adults in May or June and then die by fall. It is likely that the majority of the individuals have a one year life cycle, but it is possible that late maturing adults may produce offspring that take two summers to reach maturity. There is no evidence that this phenology pattern changes over the latitudinal range of the species.

**Parasites.**—Poinar (1985) reported an un-



Figure 38.—Karyotype (2n = 22) of subadult male *Togwoteus biceps* from near Logan, Utah.

Table 3.—Latitude versus time of year for collections of *Togwoteeus biceps*. I = immatures, A = adults. Note that 98% of the July records for the latitude 30–34° grouping came from pit traps from one locality. The label date is 3 July but probably most of the collections were from June.

Latitude	Spring			Summer			Fall			Winter		
	Mar. I, A	Apr. I, A	May I, A	June I, A	July I, A	Aug. I, A	Sep. I, A	Oct. I, A	Nov. I, A	Dec. I, A	Jan. I, A	Feb. I, A
50–55°		4, 0	21, 21	10, 17	7, 28	0, 1	1, 2	1, 1				
45–49°	35, 0	47, 0	39, 69	93, 497	11, 493	2, 73	2, 1	14, 4	23, 2	1, 0	5, 0	19, 0
40–44°		3, 0	38, 4	31, 40	25, 63	15, 77	11, 30	0, 1				
35–39°			12, 0	25, 23	6, 89	1, 22	6, 20	0, 2				
30–34°					277, 181	0, 1						
% adults	0	0	46	78	72	91	73	35	9	0	0	0

identified juvenile mermithid nematod (*Agamomermis* sp.) parasite from this harvestman. Cokendolpher (1993) recorded unidentified *Leptus* sp. mites from *T. biceps*.

CONCLUSIONS

It appears that *Togwoteeus biceps* is monotypic. The range of the species extends through much of the western prairie and mountain areas of Canada and USA. The latitudinal range is about 33–54°N, longitudinal about 98–124°W. This species has the greatest elevational range (<500 to 4100 m) and occurs at the highest elevation of any recorded harvestman in North America.

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## NOTES ON THE TAXONOMY OF SOME OLD WORLD SCORPIONS (SCORPIONES: BUTHIDAE, CHACTIDAE, ISCHNURIDAE, SCORPIONIDAE)

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**ABSTRACT.** The following new synonymies are found among the scorpions of the Old World: *Buthoscorpio* Werner 1936 = *Pocockius* Francke 1985, NEW SYNONYMY; *Androctonus* (*Leiurus*) *quinquestriatus* Ehrenberg 1828 = *Androctonus* (*Liurus*) *quinquestriatus aculeatus* Ehrenberg 1831, NEW SYNONYMY; *Euscorpium mingrelicus gamma* (Caporiacco 1950) (in part), NEW COMBINATION = *Euscorpium mingrelicus caprai* Bonacina 1980, NEW SYNONYMY. The following new homonymies are published: *Buthus* (*Hottentotta*) *hebraeus* Werner 1935, NEW HOMONYMY; *Buthus acutecarinatus judaicus* Birula 1905, NEW HOMONYMY; *Euscorpium germanus polytrichus* Hadzi 1929, NEW HOMONYMY; *Euscorpium germanus oligotrichus* Hadzi 1929, NEW HOMONYMY; *Euscorpium carpathicus oligotrichus* Hadzi 1929, NEW HOMONYMY; *Scorpio maurus subtypicus* Birula 1910, NEW HOMONYMY. The following new replacement names are introduced to replace junior homonyms: *Androctonus amoreuxii levyi* Fet, NOMEN NOVUM = *Buthus* (*Hottentotta*) *hebraeus* Werner 1935, NEW SYNONYMY; *Lychas marmoreus lucienkochi* Fet, NOMEN NOVUM = *Lychas marmoreus obscurus* Kraepelin 1916, NEW SYNONYMY; *Uroplectes fischeri caporiaccoi* Fet, NOMEN NOVUM = *Uroplectes fischeri intermedius* Caporiacco 1941, NEW SYNONYMY; *Hadogenes trichiurus wernerii* Fet, NOMEN NOVUM = *Hadogenes trichiurus paucidentis* Werner 1939, NEW SYNONYMY; *Scorpio maurus birulai* Fet, NOMEN NOVUM = *Scorpio maurus subtypicus* Birula 1910, NEW SYNONYMY. Type species are designated for *Pilumnus* C.L. Koch 1837, *Repucha* as proposed by Francke (1985), and two subgenera of *Pandinus* Thorell as proposed by Vachon (1974). An incorrect original spelling *Trichobuthus grubleri* Vachon 1941 is corrected to *T. guebleri* (a junior synonym of *Buthiscus bicalcaratus* Birula 1905). The correct date of the description for *Pectinibuthus* Fet is 1984, but not 1987. The name *Euscorpium carpathicus mesotrichus* Hadzi 1929 is a junior homonym and cannot be used.

These notes discuss some taxonomic problems within the Old World scorpiofauna. This fauna, especially in the Mediterranean area and Middle East, has been described intensively since the 18th century, often creating multiple synonymies and homonymies. A considerable effort of many generations of scorpion taxonomists (including such prominent names as T. Thorell, R.I. Pocock, E. Simon, K. Kraepelin, A. Birula, M. Vachon, O. Francke, W.R. Lourenço) led to the clarification of many nomenclatural problems; however, a number of situations exist which do not comply with the International Code of Zoological Nomenclature (ICZN 1985; further quoted as separate Articles). Below, I attempted to analyze those situations.

### FAMILY BUTHIDAE C.L. KOCH 1837

#### Genus *Androctonus* Ehrenberg 1828

*Buthus* (*Hottentotta*) *hebraeus* Werner 1935, NEW HOMONYMY (currently *Androctonus*

*amoreuxii hebraeus*) is found to be a primary junior homonym of *Buthus quinquestriatus hebraeus* Birula 1908 (currently *Leiurus quinquestriatus hebraeus*) (Article 53 of the Code), and thus is permanently invalid (Article 52) and has to be replaced. A new replacement name is introduced, *Androctonus amoreuxii levyi* Fet, NOMEN NOVUM = *Buthus* (*Hottentotta*) *hebraeus* Werner 1935, NEW SYNONYMY. Etymology: a patronym honoring the Israeli arachnologist Dr. Gershom Levy.

#### Genus *Buthiscus* Birula 1905

Vachon (1941) described *Trichobuthus grubleri* from Algeria. Later (Vachon 1942) he found this species to be a junior synonym of *Buthiscus bicalcaratus* Birula 1905. The original patronym *grubleri* was supposed to be formed from the collector's name, M. Gübler, and is therefore an incorrect original spelling [Article 32(c)]. Vachon (1952) admitted

clear evidence of an inadvertent error (*lapsus calami*). It is here corrected to *Trichobuthus guebleri* Vachon 1941; following Article 32(d)(i)(2), the letter "e" is inserted after the vowel.

#### Genus *Buthoscorpio* Werner 1936

This genus was originally described in the family Scorpionidae, with a single (type by monotypy) species *Buthoscorpio laevicauda* Werner 1936, from India. Vachon (1961) found this species to be a buthid, and a junior synonym of *Stenochirus politus* Pocock 1899 (Buthidae). Thus, the name *Buthoscorpio* Werner 1936 became a junior synonym of *Stenochirus* Karsch 1892 (type species by original designation *Stenochirus sarasinorum* Karsch 1892, from Sri Lanka).

Later, Francke (1985) discovered that Karsch's name was a junior homonym of *Stenochirus* Oppel 1862 (Crustacea). A replacement name, *Pocockius* Francke 1985, was introduced as a *nomen novum* for *Stenochirus* Karsch 1892. However, the name *Buthoscorpio* Werner 1936 is an available synonym [Article 60(b)]. Therefore, *Buthoscorpio* Werner 1936 = *Pocockius* Francke 1985, NEW SYNONYMY. This genus includes two species: *Buthoscorpio politus* (Pocock 1899), NEW COMBINATION (the type species) and *B. sarasinorum* (Karsch 1892), NEW COMBINATION.

#### Genus *Compsobuthus* Vachon 1949

Two taxa, originally described as *Buthus acutecarinatus judaicus* Birula 1905 (Middle East; type locality: Jordan and Lebanon) and *Buthus acutecarinatus werneri* Birula 1908 (Africa, Middle East; type locality: Sudan), were treated for a long time as two separate species of the genus *Compsobuthus* Vachon 1949. Levy & Amitai (1980) demonstrated that these two forms are subspecies of the same species (with an intergradation zone in Israel), assigned both subspecies to *Compsobuthus werneri* as *C. werneri werneri* and *C. werneri judaicus*. Recently, Sissom (1994) confirmed and redescribed *C. werneri werneri*.

It can be observed that *Buthus acutecarinatus judaicus* Birula 1905 is a senior synonym of *Buthus acutecarinatus werneri* Birula 1908. The situation is complicated by the fact that *Buthus judaicus* Simon 1872 (currently

*Hottentotta judaicus*) is found to be a primary senior homonym of *Buthus acutecarinatus judaicus* Birula 1905, NEW HOMONYMY (Article 53 of the Code). Therefore, the name *Buthus acutecarinatus judaicus* Birula 1905 is permanently invalid (Article 52b) and has to be replaced by the next available junior synonym which is *Buthus acutecarinatus werneri* Birula 1908 (currently *Compsobuthus werneri*). At the same time, the subspecies inhabiting Israel, Jordan, and Lebanon should be called *Compsobuthus werneri schmiedeknechti* Vachon 1949 which is the next available junior synonym based on this population (type locality: Nazareth, Israel; originally described as *Compsobuthus schmiedeknechti* Vachon 1949).

#### Genus *Leiurus* Ehrenberg 1828

The description of subspecies *Androctonus (Liurus) quinquestriatus aculeatus* Ehrenberg 1831 (as "*forma  $\alpha$  aculeata*") was based on the same type specimens and locality (Egypt and Sudan) as that of *Androctonus (Leiurus) quinquestriatus* Ehrenberg 1828 (currently *Leiurus quinquestriatus*). Therefore, *Androctonus (Leiurus) quinquestriatus* Ehrenberg 1828 = *Androctonus (Liurus) quinquestriatus aculeatus* Ehrenberg 1831, NEW SYNONYMY.

#### Genus *Lychas* C.L. Koch 1845

C.L. Koch (1837) described the genus *Pilumnus* without designating a type species or listing any species under this name. Later he (C.L. Koch 1850) found this name to be a junior homonym of *Pilumnus* Leach 1815 (Crustacea) and proposed to use instead the name *Lychas*. This was not, however, a new replacement name, since C.L. Koch (1845) described four species listed under the genus *Lychas* but did not give a separate description of this genus. This, according to Article 12(b)(5), constitutes an indication; therefore the correct date of the generic name *Lychas* is 1845, as correctly suggested by Vachon (1985) but not 1850, as used by Kraepelin (1899) and L.E. Koch (1977).

Of the four species described in 1845 (and listed also in C.L. Koch 1850), only one, *Lychas scutillus* C.L. Koch 1845, currently is included in genus *Lychas*; all three other species are synonyms of *Isometrus maculatus* (De Geer 1778). On this basis, Pocock (1899)



fixed the type species for the genus *Lychas* C.L. Koch 1845 as *Lychas scutillus* C.L. Koch 1845. I designate here the type species for *Pilumnus* C.L. Koch 1837, also as *Lychas scutillus* C.L. Koch 1845, which follows the requirements of Article 13(a).

Francke (1985) introduced *Repucha* as a replacement name for *Pilumnus* C.L. Koch 1837, and synonymized it with *Lychas*. However, since the type species of *Pilumnus* C.L. Koch was not originally designated, *Repucha* Francke also does not have a type species and therefore (being created after 1930) is not available under Francke's authorship [Article 13(b)]. I designate here the type species for *Repucha* as *Lychas scutillus* C.L. Koch 1845, which makes this generic name available as *Repucha* Fet 1997, and a junior synonym of *Lychas* C.L. Koch 1845.

*Lychas marmoreus obscurus* Kraepelin 1916, NEW HOMONYMY, from Australia, is found to be a primary junior homonym (Article 57) of *Lychas asper obscurus* Kraepelin 1913 from Africa. A new replacement name is introduced, *Lychas marmoreus lucienkochi* Fet, NOMEN NOVUM = *Lychas marmoreus obscurus* Kraepelin 1916, NEW SYNONYMY. Etymology: a patronym honoring Dr. Lucien E. Koch, the author of a revision of Australian scorpiofauna (L.E. Koch 1977); a composite word is constructed to avoid confusion with the names of two other prominent scorpion taxonomists, Carl L. Koch and his son Ludwig Koch. This subspecies is listed by L.E. Koch (1977) as a valid form.

#### Genus *Pectinibuthus* Fet 1984

Orlov & Vasilyev (1984) published Fet's description of the new genus (*Pectinibuthus*) and its only species (as "*Pectinibuthus birulai* Fet 1983") from Turkmenistan without the author's permission, without information on type material, and with several mistakes. Fet (1989) treated these names as *nomina nuda*, since the extended correct description with the information on type material was published separately (Fet 1987). However, the 1984 date satisfies all requirements for the publication, availability of both genus and species names (Articles 11, 13), and fixation of the type species by indication (by monotypy) [Article 68(d)]. It appeared in a numerous-copy brochure (Orlov & Vasilyev 1984) published by the Gorky State University (Gorky, USSR);

300 copies of it were simultaneously obtainable free of charge. The brochure is dated 1983 on the cover but was approved for print only in January 1984 (information on the back side of the cover page). Therefore, the correct date of publication for *Pectinibuthus* Fet and *P. birulai* Fet is 1984, and the correct reference to the original description is "Fet in Orlov et Vasilyev 1984".

#### Genus *Uroplectes* Peters 1862

*Uroplectes fischeri intermedius* Caporiacco 1941, NEW HOMONYMY, is found to be a primary junior homonym (Article 57) of *Uroplectes intermedius* Tullgren 1907 (which is a junior synonym of *Uroplectes xanthogrammus* Pocock 1897) (both from Africa). A new replacement name is introduced, *Uroplectes fischeri caporiaccoi* Fet, NOMEN NOVUM = *Uroplectes fischeri intermedius* Caporiacco 1941, NEW SYNONYMY. Etymology: a patronym honoring Dr. Lodovico di Caporiacco, the well-known Italian arachnologist.

#### FAMILY CHACTIDAE POCOCK 1893

##### Genus *Euscorpis* Thorell 1876

Hadzi (1929) studied three European species, *E. italicus* (Herbst 1800), *E. carpathicus* (Linnaeus 1767), and *E. germanus* (C.L. Koch 1837) from the former Yugoslavia and adjacent areas. Within each of those species, Hadzi described three "forms" which were given names *oligotrichus*, *mesotrichus* and *polytrichus*. These forms have status of subspecies [Article 45(f)]. Capra (1939) correctly recognized *E. italicus mesotrichus* Hadzi 1929 as a (primary) senior homonym of *E. germanus mesotrichus* Hadzi 1929 and *E. carpathicus mesotrichus* Hadzi 1929 [Article 52(a)]. Capra did not introduce any replacement names. None of the three subspecies described by Hadzi (1929) within *E. italicus* is currently recognized as valid; however, these names remain available junior synonyms of *E. italicus*.

All six subspecies described by Hadzi (1929) within *E. germanus* and *E. carpathicus* are primary junior homonyms. Most of these forms do not have originally designated type specimens and/or localities. Type material of Hadzi, formerly in the Slovenian Academy of Sciences in Ljubljana, is considered lost (M. Kuntner pers. comm.). For *E. carpathicus polytrichus* Hadzi 1929 (type locality unknown), Caporiacco (1950) published a replacement



name, *E. carpathicus hadzii*. The following observations can be made regarding the remaining five subspecies. *E. carpathicus oligotrichus* Hadzi 1929, NEW HOMONYMY (type locality unknown) and *E. germanus polytrichus* Hadzi 1929, NEW HOMONYMY (type locality unknown) are not diagnosable at the subspecies level and are both synonyms of *Euscorpius carpathicus* (L. 1767) (Caporiacco 1950).

*E. germanus oligotrichus* Hadzi 1929, NEW HOMONYMY (type locality unknown) and *E. germanus mesotrichus* Hadzi 1929 (type locality: Kranjska, now Slovenia) are also not diagnosable (Caporiacco 1950). Both forms were synonymized with *E. germanus* by Kinzelbach (1975). According to current division (Bonacina 1980), they may belong either to *E. germanus* (C.L. Koch 1837) or to *E. mingrelicus* (Kessler 1874).

The validity and rank of *Euscorpius carpathicus mesotrichus* Hadzi 1929 (type locality: southern Slovenia) remains unclear. Caporiacco (1950) synonymized it with *E. carpathicus tergestinus* (C.L. Koch 1837) (type locality: Trieste, Italy). Kinzelbach (1975) did not accept this synonymy and elevated Hadzi's subspecies to the species status as *Euscorpius mesotrichus* Hadzi 1929, significantly increasing its scope and range. A number of authors (e.g., Michalis & Dolkeras 1989; Lacroix 1991; Kritscher 1993) followed Kinzelbach (1975) in using the name *E. mesotrichus*, although it is a primary junior homonym and cannot be used. If this form is considered a valid species, it currently should be called *Euscorpius tergestinus* (C.L. Koch).

The subspecies *Euscorpius germanus gamma* Caporiacco 1950 was based on a series of syntypes from northeastern Italy and Slovenia. This subspecies was revised by Bonacina (1980) who synonymized part of it with the nominotypical subspecies *E. germanus germanus* (C.L. Koch), while transferring another part as a subspecies to *Euscorpius mingrelicus* (Kessler). For this latter subspecies, Bonacina (1980) introduced a replacement name, *E. mingrelicus caprai*. However, Caporiacco's name remains available even if it denotes more than one taxon (Article 17). Therefore, the correct name for this subspecies is *Euscorpius mingrelicus gamma* (Caporiacco 1950) (in part), NEW COMBINATION =

*Euscorpius mingrelicus caprai* Bonacina 1980, NEW SYNONYMY.

#### FAMILY ISCHNURIDAE SIMON 1879

##### Genus *Hadogenes* Kraepelin 1894

*Hadogenes trichiurus paucidens* Werner 1939, NEW HOMONYMY, is a primary junior homonym of *Hadogenes paucidens* Pocock 1896 (both from South Africa). A new replacement name is introduced, *Hadogenes trichiurus weneri* Fet, NOMEN NOVUM = *Hadogenes trichiurus paucidens* Werner 1939, NEW SYNONYMY. Etymology: a patronym honoring Dr. Franz Werner who made extensive contributions to scorpion taxonomy in the 1900s–1930s. The validity of this form was never challenged probably because it was forgotten; it was neither listed by Lamoral & Reynders (1975) nor discussed in the recent revision of *Hadogenes* (Newlands & Cantrell 1986).

#### FAMILY SCORPIONIDAE LATREILLE 1802

##### Genus *Pandinus* Thorell 1876

Two taxa, *Pandinoides* Vachon 1974 and *Pandinurus* Vachon 1974, were described (Vachon 1974) as subgenera of *Pandinus*; however, type species were not designated or indicated for these (non-monotypic) taxa. According to Article 13(b) of the Code, these names are not available under Vachon's authorship. I designate here their type species and retain the generic names (as described by Vachon 1974): *Pandinoides* Fet 1997 (type species *Scorpio exitialis* Pocock 1888); and *Pandinurus* Fet 1997 (type species *Pandinus militaris* Pocock 1900).

Three other valid subgenera of *Pandinus* are: the nominotypical subgenus (type species by original designation *Buthus imperator* C.L. Koch 1841), *Pandinops* Birula 1913 (type species by indication *Pandinus peeli* Pocock 1900), and *Pandinopsis* Vachon 1974 (type species by monotypy *Scorpio dictator* Pocock 1888).

##### Genus *Scorpio* Linnaeus 1758

The species *Scorpio maurus subtypicus* Birula 1910, NEW HOMONYMY (from Morocco) is found to be a primary junior homonym of *Scorpio africanus subtypicus* Kraepelin 1894 (from Sudan; currently *Pan-*



*dinus imperator subtypicus*), and therefore is a permanently invalid name (Article 52 of the Code). A new replacement name is introduced, *Scorpio maurus birulai* Fet, NOMEN NOVUM = *Scorpio maurus subtypicus* Birula 1910, NEW SYNONYMY. Etymology: a patronym honoring the famous Russian scorpionologist Dr. Alexei A. Birula (Byalynitsky-Birula).

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## DESCRIPTION OF THE MALE OF *DIPLOCENTRUS LOURENCOI* (SCORPIONES, DIPLOCENTRIDAE)

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**ABSTRACT.** The male of *Diplocentrus lourencoi* Stockwell 1988 is described and illustrated from a specimen collected west of San Pedro Sula, Honduras, and compared to the holotype female and the males of other *Diplocentrus* Peters 1861 in the region. The hemispermatophore is described, illustrated, and compared to other *Diplocentrus* in the region. Unique new characters on the male, posterolateral recesses on tergite VII, are described and illustrated. New descriptive information is given for the holotype female. Complete measurements and morphometrics are given for the male and female. A comparative diagnosis is offered based on this new information.

The original description of *Diplocentrus lourencoi* Stockwell 1988 was based on a single adult female from Río Santa Ana Canyon (3500 ft.), San Pedro Sula, Departamento Cortés, Honduras, collected during the Field Museum Expedition into Central America in the spring of 1923. Recently, Thomas G. Anton of the Field Museum (FMNH) discovered undetermined scorpion material that included an additional specimen from the expedition that was not studied previously. This specimen is an adult male collected by K. Schmidt and L. Walters on 1 April 1923 at “Mt. Camp, 4500 ft. El., W. of San Pedro Sula, Honduras,” several days after the female holotype was collected. (According to Mr. Anton [pers. comm.], “Mt. Camp” refers to the campsite location and not a geographic place name.) Examination of the holotype female was necessary to confirm that this male specimen is referable to *D. lourencoi*. This specimen brings the total number of reported diplocentrids from Honduras to a mere 12 individuals assignable to four species in two genera: *Diplocentrus coddingtoni* Stockwell 1988, *D. santiagoi* Stockwell 1988, *D. lourencoi*, and *Didymocentrus krausi* Francke 1978.

Because the male of this species is previously undescribed and distinct sexual dimorphism in diplocentrids is well documented, it is important that comparisons are made to complete the diagnosis of the species and to aid in separating *D. lourencoi* from related species. Male morphology tends to provide

more diagnostic characters for the genus at the species level than do female characters (Francke 1977).

Due to the brevity of the original description it became necessary to examine the female holotype. Upon examination of the holotype, the drawings of the female pedipalp chela in the original description were found to depict inaccurately the nature of the chelal reticulation, granulation, and keel structure. The pattern of chela reticulation and texture observed in the holotype female is extremely similar to that seen in the male, which is herein described and illustrated. In addition, the notable slenderness of the chelicerae and length of the chelical fingers of *Diplocentrus lourencoi* were not included in the original description: chelical morphometrics have been found to have diagnostic importance in diplocentrid scorpions (Francke 1977). Complete measurements for the holotype female are published here for the first time.

Nomenclature and mensuration essentially follow that of Stahnke (1970), except that chelical measurements and carinal terminology are after Francke (1975, 1977) and trichobothrial terminology is after Vachon (1974).

*Diplocentrus lourencoi* Stockwell 1988

*Diplocentrus lourencoi* Stockwell 1988: 161–163, figs. 19–24.

**Type data.**—Holotype female from Río Santa Ana Canyon (3500 ft.), San Pedro Sula,

Departamento Cortés, Honduras, 21 March 1923 (K. Schmidt and L. Walters), Capt. Field Mus. Exped., deposited in the Field Museum, Chicago; examined (*Note:* The original data label with the specimen does not indicate San Pedro Sula or Departamento Cortés; this information was thoughtfully provided in the original description by Stockwell, apparently after a thorough investigation of Honduras geography).

**Description of male.**—*Coloration (in alcohol):* Carapace dark orange brown to mahogany with weak underlying marbling of light patches. Tergites dark orange brown to mahogany, infuscate. Metasoma dark orange brown, with each segment gradually darker distally; dorsal keels at least proximally nigrocarinate; telson dark orange brown, grading to light yellow brown at subaculear tubercle. Venter of prosoma reddish brown becoming yellow brown laterally with faint infuscation; genital opercula, pectines, and basal piece yellowish. Sternites II–VI light orange brown to light yellow brown; sternite VII slightly darker. Chelicera manus light yellow brown becoming slightly darker distally with faint reticulate pattern proximally; fingers yellowish, with teeth somewhat transparent under magnification, appearing light orange brown. Pedipalp external surfaces deep mahogany gradually becoming lighter distally to light red-brown fingers; internal surfaces light yellow brown at dorsal lobe becoming darker distally. Legs dark yellow brown proximally with marbled pattern, distal segments light yellowish.

*Prosoma:* Carapace only slightly longer than posterior width: length/width ratio 1.05. Surface feebly reticulate. Anterior margin of carapace and anterior median furrow moderately coarsely granular (Fig. 1); remainder of carapace with dense fine granulation interspersed with coarser granules. Sternum with 14 setae; each genital operculum with seven setae. Coxosternal region finely punctate, somewhat lustrous; coxae sparsely setose.

*Mesosoma:* Tergites I–VI with very dense fine granulation, shagreened. Tergite VII weakly bilobed posteriorly with moderate to coarse granulation (Fig. 2). Pre-posterolateral recess moderate, shallow; posterolateral recess strong, deep (Fig. 2). Pectinal tooth count 9–10. Sternites III to VI finely punctate and somewhat lustrous, smooth. Sternite VII with

submedian carinae vestigial, smooth, provided with four pairs of setae; lateral carinae weak, smooth, provided with five pairs of setae.

*Hemispermaphore:* Lamelliform; inner margin of median lobe with a moderate ridge with four teeth. Distal lamina not broad, tapering only at distal end (Figures 3–5).

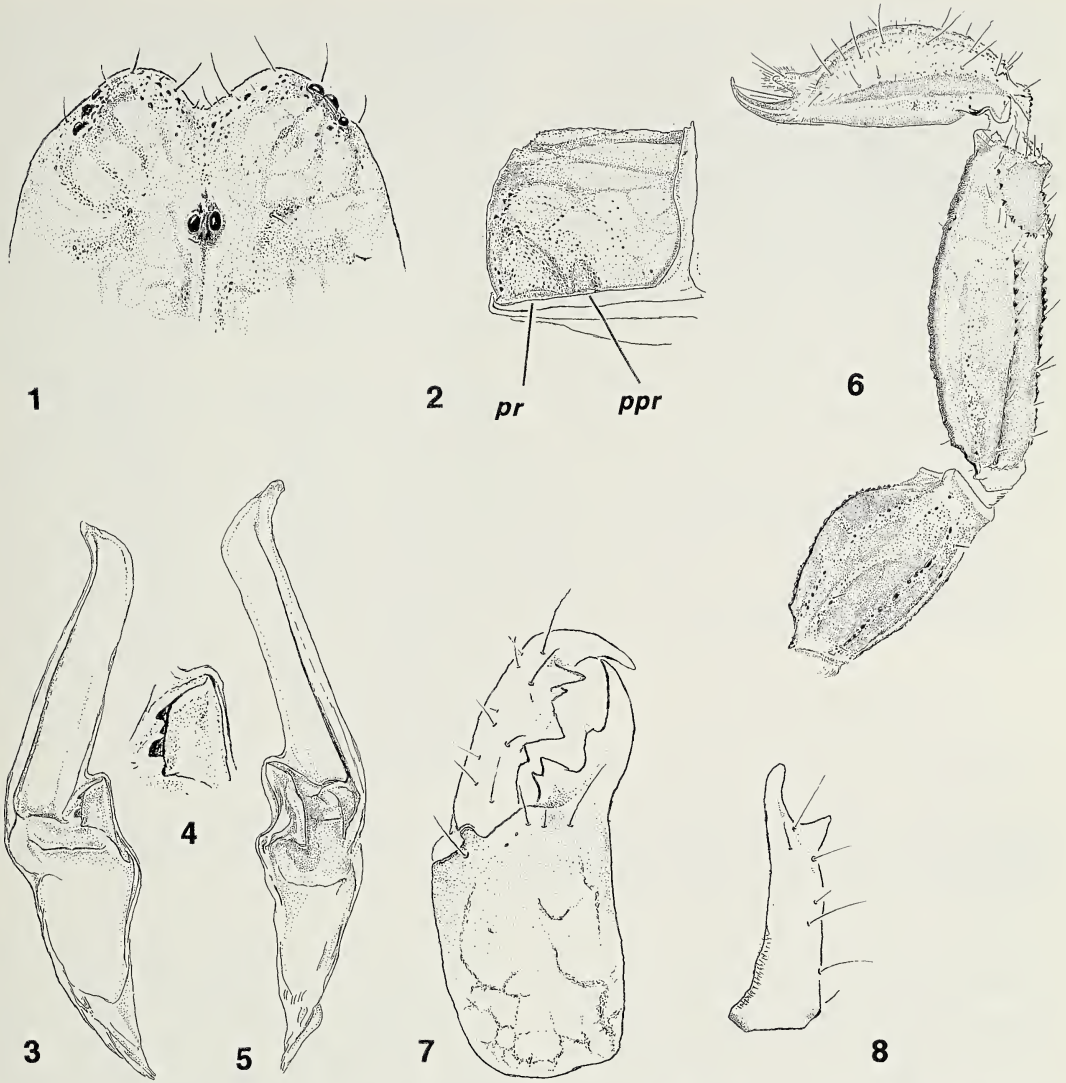
*Metasoma:* Segments I–IV: Dorsolateral carinae moderate, granular, increasing in strength on distal segments. Lateral suprmedian carinae on I–IV strong, on I–II smooth to granular, on III–IV granular throughout. Lateral inframedian carinae on I–III moderate, smooth to granular; on IV (Fig. 6) represented by an irregular row of granules. Ventrolateral carinae on I moderate, smooth; on II–IV weak, granular. Ventral submedian carinae on I and II weak, smooth to granular; on III moderate, smooth on proximal one-half, vestigial with irregularly scattered granules on distal half; reduced on IV to two narrowly separated irregular rows of granules on proximal two-thirds. Intercarinal spaces feebly reticulate. Segment V: Dorsal surface densely finely granular medially with coarser granulation laterally; dorsolateral carinae moderate, densely moderately granular; lateromedian carinae present only on anterior two-thirds, strong, granular; lateral intercarinal surfaces feebly reticulate, smooth distally (Fig. 6); ventrolateral, ventromedian, and ventral transverse carinae moderate to strong with subconical granules, with cluster of seven ventromedian granules beyond ventral transverse row.

*Telson:* Ventral surface hirsute with short, white microchaetes outnumbering light-red setae; densely covered with extremely fine granules, increasingly coarser ventrally and proximally (Fig. 6). Subaculear tubercle densely hirsute, strong, laterally compressed, subconical in profile, with three pairs of long, light-red setae.

*Chelicerae:* Dentition as in Fig. 7. Smooth and relatively long, slender; fixed finger shorter than chela width (0.82 $\times$ ); movable finger subequal to chela length (0.93 $\times$ ). Other ratios in morphometric ratios section. Ventral brushes thick, long. Teeth largely transparent with only slight coloration on *di* of movable finger; *di* and *de* not in apposition (Fig. 8).

*Pedipalps:* Trichobothria pattern Type C, orthobothriotaxic (Vachon 1974). Femur: Wider than deep, with dorsointernal and ventrointernal carinae strong, granulose; dorsoex-

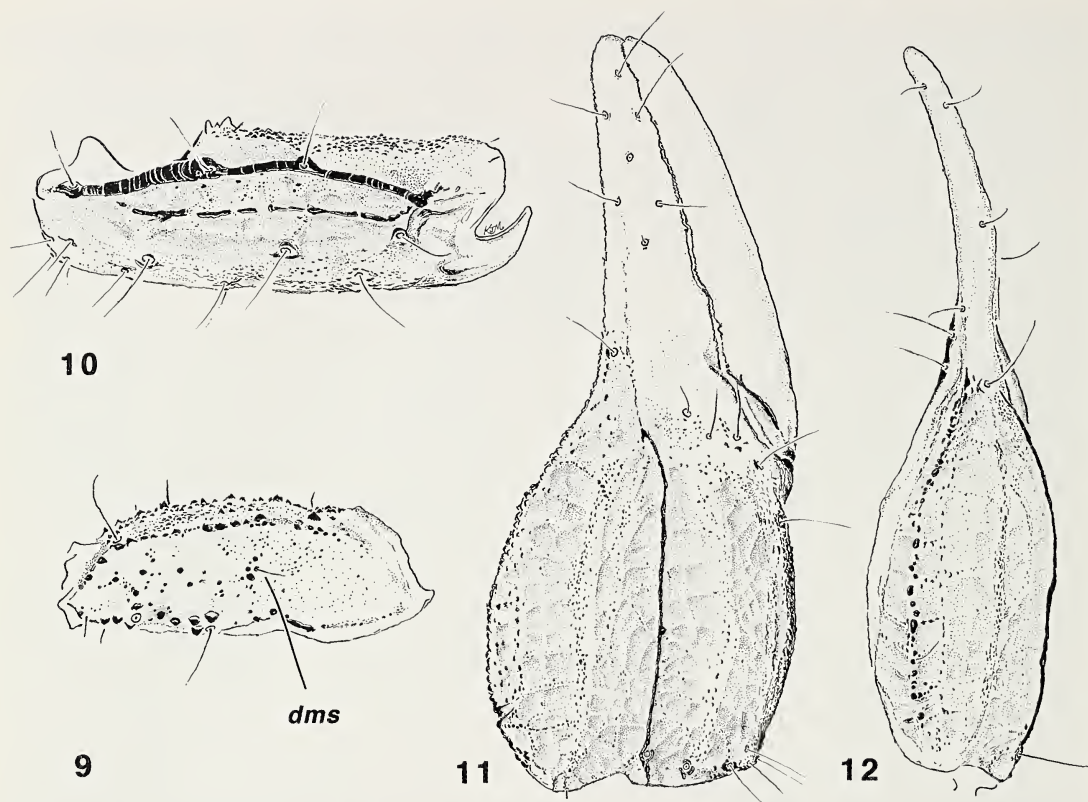




Figures 1-8.—Morphology of male of *Diplocentrus lourencoi* Stockwell. 1, Dorsal aspect of anterior region of carapace; 2, Oblique view of right lateral aspect of tergite VII, showing posterolateral recesses, *ppr* = pre-posterolateral recess; *pr* = posterolateral recess; 3, Dorsal aspect of right hemispermaphore; 4, Detail of inner margin of median lobe, showing positions of teeth; 5, Ventral aspect of right hemispermaphore; 6, Left lateral aspect of metasomal segments IV, V, and telson; 7, Dorsal aspect of left chelicera; 8, External aspect of left cheliceral movable finger.

ternal carina strong, irregularly granulose on basal two-thirds, moderately granulose on distal third; ventroexternal carina vestigial to obsolete, moderately granulose at proximal one-fifth. Dorsal surface of femur flat, with moderate and coarse granules scattered mostly for  $\frac{2}{3}$  of length, dorsomedian seta situated centrally (Fig. 9). Internal face covered with coarse granules, several of these granules rather large. Ventral surface finely granulose externally, gradually becoming coarsely granular

toward internal face. Patella: Dorsomedian keel moderate, smooth; dorsoexternal keel moderate, irregular, smooth to granular (Fig. 10); ventrointernal keel moderate, smooth to coarsely granular; ventromedian keel reduced, with scattered fine to moderate granules; ventroexternal keel moderate, smooth, distal third comprised of strong reticular costae. Chela: Palm (Fig. 11) with distinct reticulate pattern formed by weak, unpigmented costae; costae lustrous, interspersed with moderate to coarse



Figures 9-12.—Morphology of the pedipalps of *Diplocentrus lourencoi*. 9, Dorsal aspect of right pedipalp femur, *dms* = dorsomedian seta; 10, Dorsal aspect of right pedipalp patella; 11, External aspect of right pedipalp chela; 12, Dorsal aspect of right pedipalp chela.

granules; intercostal areas extremely finely granular (shagreened); dorsal margin (Fig. 12) moderately granular basally to strongly, coarsely granular to base of fixed finger; digital keel moderate and smooth for most of length, granulose and fading at trichobothrium *Dr*; dorsal and external secondary keels reduced, wide, and moderately granulose; outer surface above imaginary line between trichobothria *Esb* and *Est* reticulate, below line granulose; ventral keel strong, coarsely granular; ventrointernal keel moderate, granulose; internal surface of palm smooth, feebly reticulate with all keels greatly reduced and interspersed with fine to moderate granules. Fixed and movable fingers punctate, setose.

**Legs:** Tarsomere II spine formula 4/5 4/5: 5/5 5/5: 5/5 5/5: ?/? 5/5.

**Measurements:** Total L, 53.8; carapace L/W, 6.5/6.2; mesosoma L (specimen fragile and longitudinally compacted), 14.5; metasoma L, 26.9; telson L, 5.9. Metasomal segments: I L/W, 4.1/3.8; II L/W, 4.7/4.0; III L/W,

5.0/3.4; IV L/W, 5.7/3.0; V L/W, 7.4/2.7. Telson: vesicle L/W/D, 4.4/2.8/2.4; aculeus L, 1.5. Pedipalps: Femur L/W, 6.2/2.2; patella L/W, 6.6/1.2; chela L/W/D, 12.8/3.2/5.0; fixed finger L, 6.2; movable finger L, 8.4; palm (underhand) L, 4.4. Chelicerae: Manus L/W, 2.01/1.35; fixed finger L, 1.11; movable finger length *dil*/*de*: 1.86/1.47.

**Comparison with holotype female.**—The male is similar in appearance to the female with notable exceptions. Following are the morphometric ratios, with female ratios in parentheses. Pedipalp proportionately longer and more slender, pedipalp femur length/width, 2.82 (2.35); patella length/width, 3.14 (2.20); chela length/width, 4.00 (3.43); length/depth, 2.56 (2.26); metasomal segment II slightly shorter, length/width, 1.18 (1.22); metasomal segment V considerably longer, length/width, 2.74 (2.38). (Other ratios provided below.) Pedipalps: Granules noticeably more reduced, especially on dorsal surfaces of femur and chela, rarely encountered in diplocentrid sys-



tematics but known to occur in *Diplocentrus rectimanus* Pocock (Francke 1977). Dorsal surface of femur flat on male, distinctly convex on female. Reticulation of chela less distinct. Telson distinctly less granulose. Female slightly lighter in color, being a more yellowish brown than reddish brown, keeping in mind that the specimens are old and that some integumental separation has occurred in the female. Integument of carapace and tergites shagreened in male, somewhat lustrous in female.

**Tergite VII:** The female has a more typically shaped disc. The male, on the other hand, has strong, deep, posterolateral recesses (Fig. 2). Upon further comparisons with several species of *Diplocentrus*, *Bioculus* Stanke 1968, *Didymocentrus* Kraepelin 1905, and *Nebo* Simon 1878 (made available by W. David Sissom and Chad M. Lee), it became evident that the extreme depth of this feature is unique to at least this male specimen. Unfortunately, only a single male specimen of *D. lourencoi* is known so the utility of this feature in diplocentrid systematics will require confirmation as new material accumulates. Future descriptions should, therefore, include a brief statement regarding this feature.

**Measurements of holotype female:** Total L, 50.9; carapace L/W, 6.3/6.4; mesosoma (distended) L, 16.6; metasoma L, 22.3; telson L, 5.7. Metasomal segments: I L/W, 3.5/3.4; II L/W, 3.9/3.2; III L/W, 4.1/3.1; IV L/W, 4.6/2.9; V L/W, 6.2/2.6. Telson: Vesicle L/W/D, 4.4/2.8/2.3; aculeus L, 1.3. Pedipalps: Femur L/W, 5.4/2.3; patella L/W, 5.5/1.7; chela L/W/D, 12.0/3.5/5.3; fixed finger L, 5.1; movable finger L, 7.4; palm (underhand) L, 4.6. Chelicerae: Manus L/W, 1.95/1.47; fixed finger L, 1.11; movable finger length *dil*/*de*: 1.89/1.53.

**Morphometric ratios:** (Female ratios are in parentheses.) Carapace L/W 1.05 (0.98); metasoma II L/W 1.18 (1.22); metasoma III L/W 1.47 (1.32); metasoma V L/W 2.74 (2.39); chelicera chela L/W 1.49 (1.33), fixed finger L/chela W ratio 0.82 (0.76), movable finger L/chela L ratio 0.93 (0.97); pedipalp femur W/D (at dorsomedian seta) 1.22 (1.15), chela fixed finger L/carapace L 0.95 (0.81), movable finger L/carapace L 1.29 (1.17), chela L/W 4.00 (3.43), chela L/D 2.56 (2.26), chela W/D 0.64 (0.66), movable finger L/chela D 1.68 (1.40), movable finger L/metasma

V L 1.14 (1.19), fixed finger L/carapace L ratio 0.95 (0.81).

**Comparative diagnosis.**—The female of *Diplocentrus lourencoi* was compared to other *Diplocentrus* in the region by Stockwell 1988. Comparisons of the male with other species are based on the original descriptions and illustrations (i.e., the specimens were not examined). The hemispermatophore of *D. lourencoi* does not bear spines on the anterior margin of the median lobe as do those of *D. steeleae* and *D. ornatus*. The hemispermatophore of *D. coddingtoni* differs by lacking denticles on the inner margin of the median lobe. The pedipalp chela of *D. lourencoi* differs from that of *D. ornatus* by its greater width/depth ratio (0.64 versus 0.43) and greater length/depth ratio (2.56 versus 2.16); it differs from *D. coddingtoni* by its longer, more robust chela (length/depth ratio 2.56 versus 2.98; chela length/fixed finger length ratio 2.04 versus 2.44).

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## **GUERROBUNUS VALLENSIS, A NEW SPECIES OF HARVESTMAN (OPILIONES: PHALANGODIDAE), FROM A CAVE IN VALLE DE BRAVO, STATE OF MÉXICO, MÉXICO**

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**ABSTRACT.** *Caecoa* Šilhavý 1973 is synonymized under *Guerrobunus* Goodnight & Goodnight 1945. The third species of *Guerrobunus* is named. A taxonomic key to the species of *Guerrobunus* is provided. Two males and one female of the new species *Guerrobunus vallensis* are illustrated and described from a cave in Valle de Bravo, State of México, México.

**RESUMEN.** *Caecoa* Šilhavý 1973 se sinonimiza con *Guerrobunus* Goodnight & Goodnight 1945. Se le da nombre a la tercera especie de *Guerrobunus*. Se presenta una clave taxonómica para las especies del género. Se describen dos machos y una hembra de *Guerrobunus vallensis* nueva especie de una cueva de Valle de Bravo, Estado de México, México.

The arachnological fauna from Mexican caves is very rich and its study is in progress. Opilionids thus far reported from Mexican caves belong to the Neogoveidae, Cosmetidae, Phalangodidae, Nemastomatidae and Sclerosomatidae (= Gagrellidae). The Phalangodidae has the highest number of cave-adapted species world-wide (Rambla & Juberthie 1994) as well as in Mexico (Reddell 1981); seven described by Goodnight & Goodnight (1945, 1953, 1971, 1973), nine by Šilhavý (1974, 1977) and one each by Pickard-Cambridge (1904) and Shear (1977). Seven of these phalangodids are true eyeless troglobites: *Troglostygnopsis anophtalma* Šilhavý 1973 and *Mexotroglinus sbordonii* Šilhavý 1977 from Chiapas; *Troglostygnopsis inops* (Goodnight & Goodnight 1971) from Tamaulipas; *Hoplobunus apocalensis* Goodnight & Goodnight 1973 and *Neogovea mexasca* Shear 1977 from Oaxaca; *Hoplobunus planus* Goodnight & Goodnight 1973 from San Luis Potosí; and *Caecoa arganoi* Šilhavý 1973 from Veracruz.

During explorations of the caves in the

State of Mexico, three phalangodids that have eyes with clear cornea and unpigmented retina were collected. Because these specimens resemble *Guerrobunus minutus* Goodnight & Goodnight 1945 and *Caecoa arganoi*, a study was undertaken to determine the identity of the new specimens and the relationship of the two monotypic genera. Herein the new specimens are described as a new species and *Caecoa* is synonymized under *Guerrobunus*.

In 1945, Goodnight & Goodnight described the new genus *Guerrobunus* to contain their new species, *minutus*. Later, those same authors (1953) synonymized *Guerrobunus* (along with 14 other genera) under *Cynortina* Banks 1909. Realizing that *Cynortina* was preoccupied, Goodnight & Goodnight (1983) transferred the species of "*Cynortina*" known from Costa Rica to the next oldest genus, *Dapessus* Roewer 1933. This action resulted in those authors newly synonymizing seven genera (formerly listed as synonyms of *Cynortina*) and left seven of the genera which they had synonymized in 1953 unplaced. At that time, they also revalidated *Stygnoleptus* Banks

1914 and newly synonymized four other genera under *Stygnoleptus*. *Stygnoleptus* and three of these genera had previously (1953) been considered by them to be synonyms of *Cynortina*.

Three genera (*Azaca* Goodnight & Goodnight 1942, *Ethobunus* Chamberlin 1925, and *Guerrobunus*) synonymized under *Cynortina* in 1953 should have been listed as synonyms of *Dapessus* by Goodnight & Goodnight (1983), but they were not. Although *Azaca* and *Ethobunus* are known from Costa Rica and Panama, respectively; neither were mentioned in the Goodnight & Goodnight (1983) publication on the phalangodids of Costa Rica and will have to await further study to determine their true identities. Interestingly, the female and only known specimen of *Azaca longa* (Goodnight & Goodnight 1942) was collected on the same day, location, and by the same person as the two known specimens (both males) of *Dapessus parallelus* (Goodnight & Goodnight 1942). The lack of a listing of *Ethobunus* with *Dapessus* was questioned in the manuscript review by Cokendolpher (7 November 1981) of the paper by Goodnight & Goodnight (1983), and therefore it can be assumed that they had changed their mind on the 1953 synonymy. Furthermore, if *Ethobunus* is a synonym of *Dapessus*, it is the older name and would require a shifting of all specific names currently listed under *Dapessus*.

The rediagnosis of *Dapessus* by Goodnight & Goodnight (1983) clearly excludes *Guerrobunus* because of the higher number of tarsal elements in species of *Dapessus*. Furthermore, the male and female genitalia differ greatly.

*Guerrobunus* Goodnight & Goodnight

*Guerrobunus* Goodnight & Goodnight 1945:1.  
*Caecoa* Šilhavý 1974:189 (new synonymy).

**Diagnosis.**—Small to medium sized phalangodids, body length 1.6–3.0 mm, cephalothorax narrower anteriorly; with several obtuse tubercles on anterolateral corners. With five distinct thoracic areas, first without a median line, three free abdominal tergites. Body and leg surfaces without spines, smooth or with small granulations and tiny setae. Eye mound hemispherical, without armament, with or without eyes, at the anterior margin or slightly removed. Maxillary lobes of second

coxae with ventral projections variable in size. Spiracles not visible. Tarsal segments: 3:4:4(5):5, both distitarsi I and II with two segments. Penis with sclerotized truncus, stylus and glans soft; truncus with paired terminal ventral apophyses, sometimes also with dorsal pair of apophyses. Ovipositor short, with many setae and pair of apophyses at the distal end.

Key to the Species of *Guerrobunus*

- 1a. Eyes absent, large ventral projections on maxillary lobes of coxae II present (Šilhavý 1973, fig. 40) (from State of México)..... *G. arganoi*
- 1b. Eyes present (retina may be unpigmented), projections on maxillary lobes small (Fig. 9)..... 2
- 2a. Retina of eyes darkly pigmented, eye mound with small rounded tubercles, male body length less than 1.7 mm (from Guerrero) ..... *G. minutus*
- 2b. Cornea clear, retina unpigmented, eye mound smooth, male body length more than 2.5 mm (from State of México) ..... *G. vallensis* new species

*Guerrobunus minutus*  
Goodnight & Goodnight

*Guerrobunus minutus* Goodnight & Goodnight 1945:1.

*Cynortina minutus*: Goodnight & Goodnight 1953: 15 (by implication).

**Comments.**—Examination of the female holotype (from American Museum of Natural History) revealed that the ovipositor had been removed and is apparently lost. The “female” paratype (Universidad Nacional Autónoma de México) was also examined and determined to be a male. The penis was not illustrated or described because the curator of the museum did not allow the dissection.

Goodnight & Goodnight (1977) described a new species, *Cynortina minutus* from Belize which was a secondary homonym of *Cynortina* (= *Guerrobunus*) *minutus*. As they are no longer considered to be congeneric they are no longer homonyms requiring a replacement name.

*Guerrobunus vallensis* new species  
Figs. 1–10

**Diagnosis and comparisons.**—Medium sized (male 2.6 mm body length), ventral projections on maxillary lobes of coxae II small;



Table 1.—Appendage lengths (mm) of male holotype/male paratype of *Guerrobunus vallensis* new species.

Segment	Pedipalp	Leg I	Leg II	Leg III	Leg IV
Trochanter	0.16/0.16	0.16/0.20	0.20/0.20	0.20/0.20	0.24/0.22
Femur	0.76/0.72	0.86/0.90	1.10/1.18	0.90/0.90	1.06/1.16
Patella	0.50/0.50	0.34/0.36	0.44/0.44	0.30/0.30	0.40/0.44
Tibia	0.48/0.46	0.54/0.60	0.94/1.00	0.64/0.64	0.94/0.98
Metatarsus	—	0.60/0.68	0.90/0.98	0.84/0.84	1.16/1.24
Tarsus	0.50/0.50	0.54/0.58	1.04/1.16	0.60/0.62	0.74/0.80
Totals	2.40/2.34	3.04/3.32	4.62/4.96	3.48/3.50	4.54/4.84

coxae I with two tubercles anteriorly (larger in female), eyes present, corneas clear, retina unpigmented; ocular tubercle smooth; penis without paired apophysis on truncus dorsally. *Guerrobunus vallensis* new species appears to be closely related to *Guerrobunus minutus* but the former differs by the lack of low tubercles on the free tergites, the absence of pigment in the eyes and the total length of the body. The general structure of the penis of *G. vallensis* is similar to that of the male paratype of *G. minutus*. A detailed study of the paratype was not possible because the specimen could not be dissected, but the portion of the glans which is extending beyond the operculum appears very similar to *G. vallensis*. The penis of *Guerrobunus arganoi* (Šilhavý 1973, fig. 41) is also similar to that of *G. vallensis*. The differences between them are: the number of setae below the ventral plate, the stylus in *G. vallensis* is blunt with projections, it is pointed in *G. arganoi* with two lamella on the stylus; there are ten setae between blades in *G. vallensis* whereas *G. arganoi* has eight. Other difference is: pedipalp of male *G. vallensis* has three seta-bearing tubercles on patella, in *G. arganoi* is one.

**Type data.**—Male holotype, female allotype and male paratype from Cueva del Diablo, Valle de Bravo, State of México, México; 25 April 1990, I. Vázquez. Male holotype and female allotype deposited in the arachnologi-

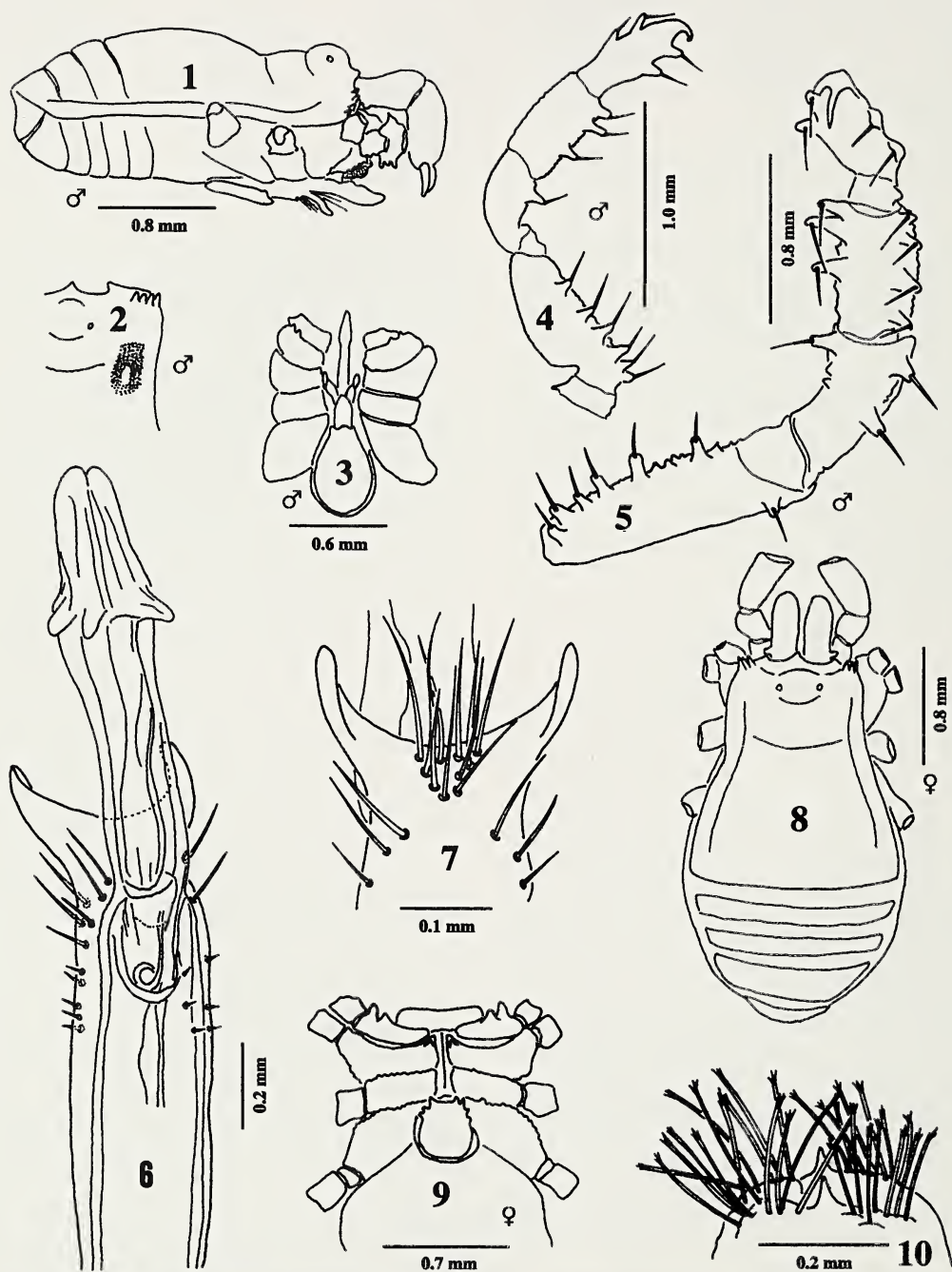
cal collection of Laboratorio de Acarología of Instituto de Biología, UNAM. Male paratype deposited at the American Museum of Natural History.

**Description (measurements in mm).**—

**Male:** Total length (without chelicerae) 2.60, width 1.40; scute length (prosoma) 1.80, 1.40 wide at boundary with free tergites. Length of legs in Tables 1, 2. Anterolateral corners of cephalothorax each with a row of four obtuse tubercles, extending laterally (Fig. 2); thoracic tergites almost indistinct (Fig. 1), only visible in lateral view. Ocular tubercle rounded, not cone-shaped, close to anterior margin of prosoma; eyes placed on each side of ocular tubercle (Fig. 1). Low hump behind ocular tubercle; free tergites without rows of small tubercles. Pedipalps (Figs. 4, 5) with spine-bearing ventrolateral tubercles: trochanter with one, femora with seven, patella with three, tibia with seven, tarsus with four. Maxillary lobes of second coxae not distinct, with one small tubercle on each, as in female (Fig. 9); coxae I with two tubercles anteriorly. Tarsal segments 3:4:5:5; distitarsus I with two segments, II with three segments (both males same). Pedipalp lengths in Table 1. Color light red to orange, except leg tarsi and eyes white. Body and legs finely granulated. Penis (Fig. 6) with two visible parts: glans blunt, with lateral projections, truncus cylindrical, oval in cross section, with a pair of sclerotized blades

Table 2.—Leg lengths (mm) of the species of *Guerrobunus*.

Taxa	Leg I	Leg II	Leg III	Leg IV
<i>Guerrobunus minutus</i> (holotype female)	2.20	3.62	2.50	3.60
<i>Guerrobunus vallensis</i> (allotype female)	4.40	5.20	3.70	5.20
<i>Guerrobunus vallensis</i> (holotype male)	3.14	3.84	3.42	4.42
<i>Guerrobunus arganoi</i> (holotype male)	4.20	6.70	4.50	6.40



Figures 1–10.—*Guerrobunus vallengis* new species. 1–7, Male holotype. 1, Lateral view; 2, Dorsal view of prosoma (right corner), with detail of granulation; 3, Ventral view, genital operculum with penis; 4, Right pedipalp, lateral view; 5, Right pedipalp, medial view; 6, Distal part of penis, dorsal view; 7, Distal part of truncus with detail of setae, ventral view. 8–10, Female allotype. 8, Dorsal view; 9, Ventral view, genital operculum and coxae; 10, Distal end of ovipositor.



Table 3.—Comparison of males of the species of *Guerrobunus* (scute length of *G. arganoi* obtained by measuring Šilhavý 1973: fig. 42).

	<i>Guerrobunus minutus</i>	<i>Guerrobunus vallensis</i>	<i>Guerrobunus arganoi</i>
Scute length	1.06	1.80	1.9
Total length	1.62	2.60	2.60
Pedipalp segment ratios	7:4:7:6	7:3:7:4	7:2:6:4
Pedipalp length	1.90	2.44	2.30
Tarsal segments	3:4:5:5	3:4:5:5	3:4:4:5
Distitarsus I:II	2:2	2:3	2:2
Eyes	present/pigmented	present/no color	absent

(= ventral plate); truncus with five pairs of tiny setae below the paired blades of ventral plate. Ventrally, between the blades, are ten long and thick setae in a triangular arrangement (Fig. 7). Penis 1.29 long; glans plus stylus 0.75 long, truncus 0.54 long; with four paired dorsal setae just below blades, and three pairs of ventral setae; six short spiny setae are on each side of truncus below glans. Stylus blunt, maximum width 0.20 (Fig. 7). Genital operculum 0.62 long, 0.48 wide, with 14 pairs of setae and one apophysis on each anterolateral corner (Fig. 5).

*Female*: Total length 2.40; scute 1.54 long, 1.50 wide at the boundary with abdomen. Leg lengths as in Table 2. Anterolateral corners of prosoma each with a row of three obtuse tubercles (Fig. 3). General structure of prosoma and abdomen as in male. Spination of pedipalps as in male (Figs. 4, 5). Tarsal segments: 3:4:5:5; distitarsus I and II with two segments each. Tubercles on coxae I more robust than in male (Fig. 9). Color light red, leg tarsi and eyes white. Genital operculum almost as wide as long with three or four spine-like apophyses on each anterolateral corner (Fig. 9). Distal end of ovipositor (Fig. 10) with 29 long setae (each with 3–5 tips), arranged in four groups, three with 7 and one with 8 setae; two spine-like apophyses between setae groups.

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## **KAIRA IS A LIKELY SISTER GROUP TO METEPEIRA, AND ZYGIELLA IS AN ARANEID (ARANEAE, ARANEIDAE): EVIDENCE FROM MITOCHONDRIAL DNA**

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**ABSTRACT.** Various authors have offered three alternative hypotheses of phylogeny which suggest different sister groups to the orb-weaving spider genus *Metepeira*. In one case *Kaira* is sister genus to *Metepeira*, and *Zygiella* is sister to *Kaira* plus *Metepeira*; in another case, *Kaira* is sister genus to *Metepeira*, but *Zygiella* is a tetragnathid, and thus unrelated at this level of analysis; and in the last case, *Zygiella* is close to *Metepeira*, but this time *Kaira* is not closely related. To resolve among these conflicting hypotheses, six species of orb-weaving spiders were sequenced for mitochondrial DNA encoding a portion of the 12S ribosomal subunit. These data were analyzed with data from two tetragnathid orb-weavers to estimate the phylogenetic relationships among these spiders and to determine which genus is a likely sister group to *Metepeira*. Phylogenetic analysis using parsimony supports the hypothesis that *Kaira* is a likely sister group to *Metepeira* and that *Zygiella* is in the family Araneidae rather than the family Tetragnathidae.

Relationships among orb-weaving spiders are, in general, poorly understood (Coddington & Levi 1991). In particular, it is not known which genus within the araneids is most closely related to the genus *Metepeira* F.P.-Cambridge 1903. Such information is valuable to a phylogenetic analysis of *Metepeira* (about 40) species because it uncovers ancestral character states and shows patterns of character evolution among species (Madison et al. 1984). It is our intention in this paper to compare 12S mtDNA sequences of several selected taxa in order to determine which among them is the closest outgroup to *Metepeira*.

Scharff & Coddington (in press) hypothesize that *Kaira* O.P.-Cambridge 1889 and *Metepeira* are sister groups because both genera share the loss of the stipes and have a median apophysis with a pair of prongs and a toothed anterior margin (compare fig. 82 with fig. 127 in Levi 1977). Thus, we targeted *Kaira* as a potential sister group to *Metepeira*. Somewhat similar median apophyses are also found in *Aculepeira* Chamberlin & Ivie 1942 and *Amazonpeira* Levi 1989, but that of *Kaira* is the most similar. Genitalic and somatic characters in *Amazonpeira* and *Aculepeira* align them closer to *Araneus* Clerck 1757 rather than to *Metepeira* (Levi 1977, 1989, 1993).

Simon (1895), who was one of the first arachnologists to discuss relationships among orb-weaving spiders in detail, did not consider *Kaira* and *Metepeira* to be closely related. His classification created four sub-families within what he called the Argiopidae (= Araneoidea), including Argiopinae (= Araneidae), which contained 28 "groups", two of which were Poltyeae and Araneae. The Poltyeae group contained *Kaira*; the Araneae group consisted of four "series", largely defined by eye arrangements. Many species which today are called *Araneus*, as well as some species affiliated to *Larinioides* Caporiacco 1934, were placed in series number 2. *Metepeira* and *Zygiella* F.O. Pickard-Cambridge 1902 were placed in series number 3. (Fig. 1, right column).

*Zygiella* is another genus which we have targeted as a candidate sister group to *Metepeira*. Scharff & Coddington (in press) agree with Simon that *Zygiella* is close to *Metepeira* based on their morphological cladistic analysis. Coddington (1990) suggests that *Zygiella*, which has a radix, distal hematodocha, and terminal apophysis, belongs to the Araneidae (Fig. 1, middle column) and not the Tetragnathidae. This placement is in keeping with three synapomorphies that are thought to unite the Tetragnathidae, yet are absent in *Zygiella*:



(Levi) (Scharff & Coddington) (Simon)

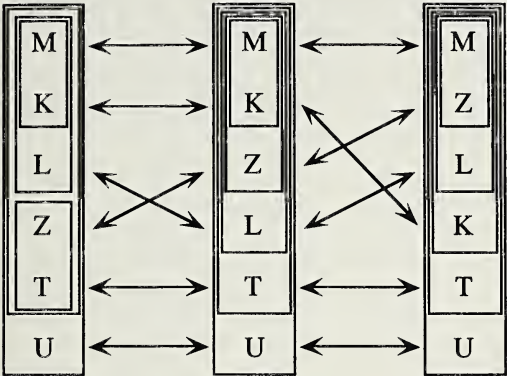


Figure 1.—Schematic diagrams illustrating three hypotheses of relationships for six orb-weaving taxa; hierarchical relationships are depicted as nested sets of Venn diagrams. Left column, hypothesis of Levi (1977, 1980); middle column, hypothesis of Scharff & Coddington (in press); right column, hypothesis of Simon (1895). Abbreviations: M, *Metepeira*; K, *Kaira*; Z, *Zygiella*; L, *Larinioides*; T, *Tetragnatha*; U, *Uloborus*.

apical tegular sclerites, loss of the median apophysis, and a conductor that wraps a free embolus (Hormiga et al. 1995). In contrast, Levi (1980) considers *Zygiella* and *Metepeira* not to be closely related. He placed the former in the Metine group of the Tetragnathidae based on the closely spaced eyes and the conical tibia (Fig. 1, left column).

To help decide among the hypotheses of Levi (Fig. 1, left column), Coddington & Scharff (Fig. 1, middle column), and Simon (Fig. 1, right column), we sequenced 12S ribosomal mtDNA from two individuals representing different species of *Metepeira*, and one individual from each of *Kaira*, *Zygiella*, *Larinioides*, and *Uloborus* Latreille 1809. These sequences were analyzed with Gillespie et al.'s (1994) data for *Tetragnatha* Latreille 1804 and *Doryonychus* Simon 1900 (family Tetragnathidae). Obviously, these eight taxa form an extremely limited sample, but the intention here is to help us select among the three main taxonomic hypotheses relating to *Metepeira* rather than to attempt a comprehensive analysis of the Araneidae.

METHODS

The six female spiders chosen for mtDNA extraction, amplification, and sequencing

were: *Metepeira daytona* Chamberlin & Ivie 1942, from Flagler Beach, Florida (29°37'N, 82°23'W); *Metepeira minima* Gertsch 1936, from Tamaulipas, Mexico (22°30'N, 99°4'W); *Kaira alba* (Hentz 1850), from Lake Lochloosa, Florida (29°37'N, 82°23'W); *Zygiella atrica* (C.L. Koch 1843), from Nahant, Massachusetts (42°25'38.7"N, 70°56'9.1"W); *Larinioides sclopeteria* (Clerck 1757), from Cambridge, Massachusetts (42°20'N, 71°6'W); and *Uloborus glomus* Walckenaer 1842, from Sherman, Connecticut (41°34'30"N, 73°31'16"W). Specimens were collected in 80% or 100% ethanol. Vouchers were deposited at the Museum of Comparative Zoology.

Tissue for extraction was dissected primarily from the prosoma: the carapace was lifted away, tissues were removed, and in many cases the carapace replaced so that the specimen appeared unaltered. For some smaller specimens, muscle fibers were also taken from the chelicerae and femora. Care was taken to exclude the cuticle which, if present, could hinder amplification (J.K. Wetterer pers. comm.).

Using chilled glass homogenizers, tissues were ground twice in 100 µl of 50 mM Tris-Cl, 20 mM EDTA, and 2% SDS. To digest the proteins, the extractions were incubated with 2 µl of 100 ng/ml proteinase K in a 60 °C oven for 1 h. To remove cell walls and residual ionic compounds, 100 µl of saturated NaCl were added. The extractions were cooled on ice for 30–70 min and then centrifuged for 15 min at 4 °C. The supernatant was retained and the DNA was precipitated with 100% EtOH, washed with 70% EtOH, dried in a centrifuge under vacuum, and resuspended in 100 µl 1xTE (10mM Tris-HCl and 1 mM EDTA).

A 257 bp region of the third domain of the 12S ribosomal subunit was amplified and sequenced for most taxa using primers 12St-L and 12Sbi-H (Croom et al. 1991). Mitochondrial DNA from *U. glomus* failed to work with 12St-L, so 12S-U [a degenerate arthropod-specific primer designed by D. Fitzpatrick (5'-TGTTT(AT)(AGT)TAATCGA(ATC)(AT)(ACT)T(AC)CACG-3')] was used instead. Two µl of template were used in 100 µl PCR reactions (50 mM KCl; 10 mM Tris-HCl; 0.1% Triton® X-100; 2.5 mM MgCl<sub>2</sub>; 0.5 µM of each primer; 2.5 units of Taq; and 0.2 mM dNTP) and cycled 30–35 times (45 sec at 94

Table 1.—Genetic distances among different species of orb-weavers. For each pairwise comparison, corrected percent distances [based on the Kimura two-parameter model (Li et al. 1985) and generated by Heap Big (Palumbi, unpub. program)] appear above the diagonal, percent transversions below the diagonal. Column headings, *M. day* = *Metepeira daytona*, *M. min* = *Metepeira minima*, *K. alb* = *Kaira alba*, *Z. atr* = *Zygiella atrica*, *L. scl* = *Larinioides sclopetaria*, *U. glo* = *Uloborus glomus*, *D. rap* = *Doryonychus raptor*, *T. per* = *Tetragnatha perreira*.

	<i>M. day</i>	<i>M. min</i>	<i>K. alb</i>	<i>Z. atr</i>	<i>L. scl</i>	<i>U. glo</i>	<i>D. rap</i>	<i>T. per</i>
<i>M. daytona</i>	—	13	18	31	30	45	49	44
<i>M. minima</i>	3	—	21	35	28	45	57	48
<i>K. alba</i>	9	7	—	27	25	44	53	41
<i>Z. atrica</i>	18	18	18	—	25	39	49	32
<i>L. sclopetaria</i>	17	14	16	17	—	44	39	36
<i>U. glomus</i>	24	23	27	24	27	—	43	42
<i>D. raptor</i>	27	27	28	26	25	24	—	28
<i>T. perreira</i>	23	23	23	18	22	26	16	—

°C; 60 sec at 42 °C; 90 sec at 72 °C). The PCR products were purified on a low melt agarose gel: bands corresponding to DNA of the appropriate length were cut from the gel, and DNA was isolated from the agarose using phenol or spin columns (QIAquick, by QIAGEN®). The PCR product was sequenced in both directions using DyeDeoxy™ termination (Perkin-Elmer Kit) with the same primers used in amplification. Sequence products were purified with CENTRI-SEP columns (Princeton Separations, Inc.) and then run on a ABI 370A autosequencer (Applied Biosystems, Inc.). Chromatogram sequence data generated by the autosequencer were edited by eye using SeqED (Applied Biosystems, Inc.).

Sequence data collected by Gillespie et al. (1994) using the same primers on two Hawaiian tetragnathid species, *Tetragnatha perreira* Gillespie 1991 from Oahu and *Doryonychus raptor* Simon 1900 from Kauai, were added to our data set and aligned using Clustal V (Higgins et al. 1992). The resulting alignment was further adjusted by hand and cropped to form a character matrix using SeqApp (Gilbert 1994). Corrected pairwise percent distances based on the Kimura two-parameter model (Li et al. 1985) were calculated using the program Heap Big (Palumbi unpub. program). An exhaustive search for the most parsimonious tree and bootstrap analysis were performed using PAUP (Swofford 1991) on sequence characters for all eight species, holding *U. glomus* as the outgroup. Trees were compared and manipulated with MacClade (Maddison & Maddison 1992).

# RESULTS

The resulting character matrix is 208 bases long (Fig. 2). An exhaustive search using PAUP (Swofford 1991) yields two most parsimonious trees, each 227 steps long, C.I. with all characters, 0.75; C.I. with uninformative characters excluded, 0.67; and R.I. of 0.54. The two trees disagree only in whether *L. sclopetaria* is more closely related to *K. alba* plus *Metepeira* or whether it is more closely related to *Z. atrica*. The strict consensus of these two trees is illustrated in Fig. 4. Although pairwise genetic distances (Table 1) are quite high, skewness test statistic ( $g_1$ ) calculated by PAUP is -0.81, which is statistically significant ( $P < 0.01$ ), indicating that there is, nonetheless, strong phylogenetic signal (Hillis & Huelsenbeck 1992). Furthermore, an exhaustive search with *U. glomus* excluded results in a single most parsimonious tree with *Z. atrica* most closely related to *Metepeira* plus *K. alba*—a result that is still compatible with Fig. 4.

Of the 76 unambiguous changes on the tree (i.e., character state changes that optimize to a single, specific branch segment), 31 are transitions (purine to purine or pyrimidine to pyrimidine) and 45 are transversions (purine to pyrimidine or pyrimidine to purine). This paradoxically low ratio of transition to transversion events increases with decreasing branch lengths (Fig. 3) and therefore is evidence for multiple hits and saturation between distant relatives (Simon et al. 1994). However, a transition to transversion ratio of 0.69 is still with-





Figure 2.—Matrix of 208 characters from aligned 12S ribosomal mtDNA sequences. Data for eight orb-weaving taxa are represented, two of which (*Doryonychus raptor* and *Tetragnatha perreira*) were published in Gillespie et al. (1994).

in the range of other comparable and successful phylogenetic analyses, such as 0.61 for the analysis of tetragnathid relationships by Gillespie et al. (1994).

DISCUSSION

Our data support the Scharff and Coddington hypothesis (compare Fig. 4 with Fig. 1, middle column) and thus provide evidence that *Kaira* is, indeed, a likely sister-group to *Metepeira*. Despite the fact that *Metepeira* is a morphologically homogeneous taxon with a restricted distribution, thus presumably with a relatively recent inception, the within-*Metepeira* distances are not much shorter than those between *Metepeira* and *Kaira* (Table 1). Furthermore, the *Kaira-Metepeira* clade is supported by 94% of 1000 bootstrap replicates and eight unambiguous apomorphies (Fig. 4). Nonetheless, the branch lengths between clades seem more evenly spaced than what one might at first expect, given that some unite closely related taxa, whereas others unite

distantly related taxa. However, this may merely reflect multiple substitutions, in which long genetic distances are vastly underestimated when new mutations occur at the same sites as the old mutations. Evidence for this occurrence can be seen in the attenuation of

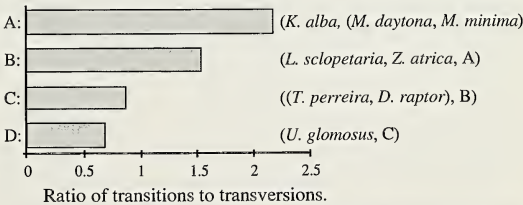


Figure 3.—Ratio of unambiguous transitions to unambiguous transversions for increasingly inclusive clades as calculated by MacClade (Maddison & Maddison 1992). Clade A includes *Kaira alba*, *Metepeira daytona*, and *M. minima*; clade B includes *Larinioides sclopetaria*, *Zygiella atrica*, and clade A; clade C includes *Tetragnatha perreira*, *Doryonychus raptor*, and clade B; clade D includes *Uloborus glomusos* and clade C.

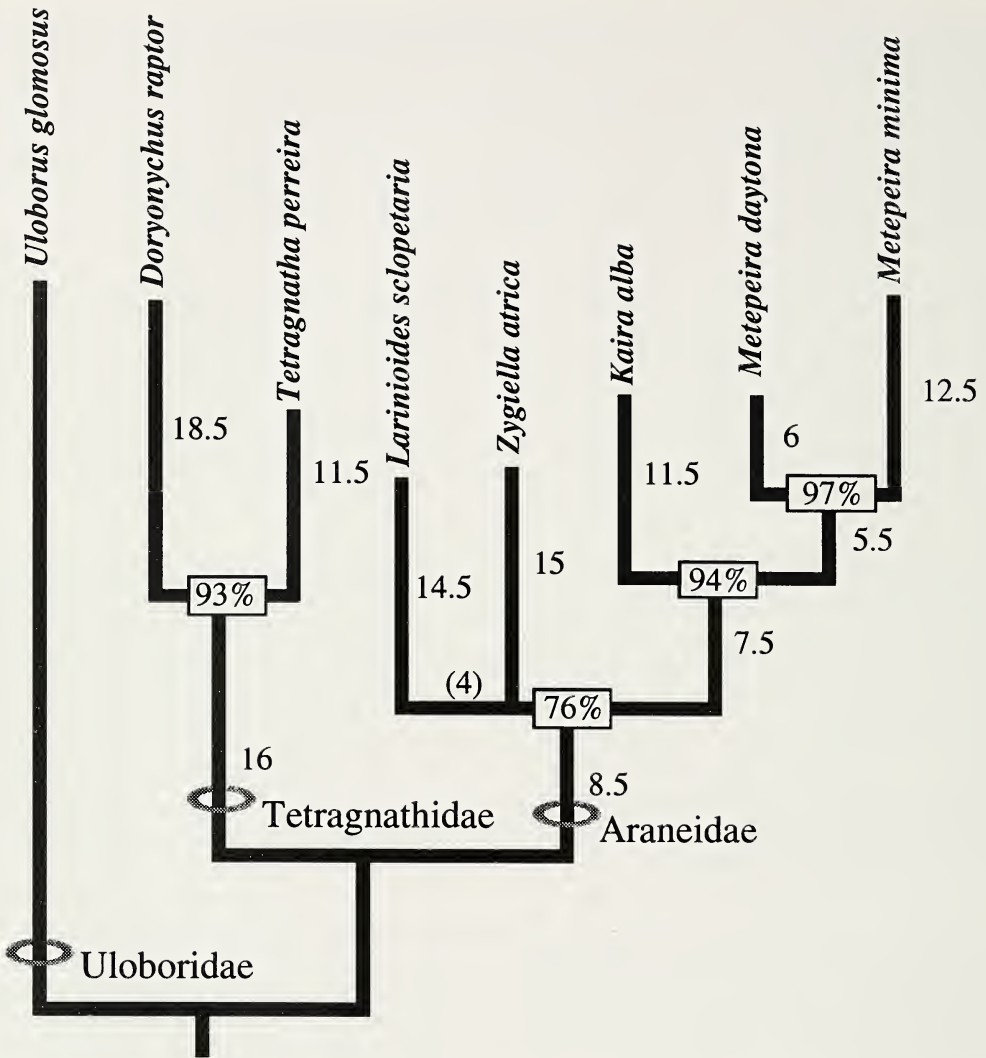


Figure 4.—Strict consensus tree of the two most parsimonious phylogenetic trees from 208 bases of the 12S ribosomal mtDNA subunit (tree length = 223+ steps; C.I. using all characters = 0.79; C.I. using informative characters only = 0.75). Figures adjacent to each branch indicate the number of unambiguous character changes averaged between the two most parsimonious trees. The figure in parentheses indicates the number of unambiguous character changes between where *L. sclopetaria* or *Z. atrica* branch from the main stem in either shortest tree. Percentages are bootstrap values for each node from 1000 replicates.

the transition to transversion ratio when measured over increasingly inclusive clades (Fig. 3). Although transitions occur more frequently than transversions, accumulation of transversions in older, longer branches will mask the activity of transitions (Simon et al. 1994). The pronounced attenuation of the transition to transversion ratio in our data suggest that the *Kaira* is actually closer to *Metepeira*, yet farther from the other taxa, than what the tree would appear to show. The same can be said

for the separation between the araneids and the tetragnathids.

The close relationship between *Kaira* and *Metepeira*, as evidenced from our results, indicates that the shared flagellated median apophysis, as well as other genitalic characters, are likely to be homologous structures. Despite this particular similarity, *Kaira* and *Metepeira* share few other morphological features. *Kaira* has evolved numerous autapomorphies as a result of its highly specialized



predatory behavior. Convergent with *Mastophora* Holmberg 1876, *Kaira* has forgone orb-weaving, and is thought to emit pheromones that mimic those of female moths (Levi 1994; Stowe 1986). Thick, stubby setae on *Kaira*'s legs are presumably used to grab moths in flight, while a large array of tubercles on *Kaira*'s abdomen are thought to conceal or protect the exposed spider while it is in its hunting posture. In contrast, *Metepeira* has neither specialized leg setae nor abdominal tubercles, and it weaves a very distinctive web which combines orb and scaffolding with associated aerial retreat.

Identifying the sister group to *Metepeira* can help clarify phylogenetic structure and character evolution within the genus. Levi (1977) divided *Metepeira* species north of Mexico into two groups: *M. labyrinthea* and *M. foxi*. Species in the former group have a white line on a black sternum and a short keel on the median apophysis. Species in the latter group have a uniform sternum and a distal tuberculate keel on the median apophysis. Levi (1977) admitted that it "is difficult at present to decide which of these species groups is the derived and which the more primitive". Indeed, one needs an outgroup in order to determine which species group contains species arising basally and retaining symplesiomorphic characters, and which species group contains species arising more distally and sharing synapomorphic characters.

With *Kaira* as an outgroup to *Metepeira*, we can infer that the character states that define the *M. foxi* species group are primitive, and thus species in this group may arise basally within the genus *Metepeira*. Indeed, the distal tuberculate keel on the median apophysis is similar to modifications in the median apophysis of *Kaira* (compare figs. 82, 91–127 in Levi 1977). Furthermore, *Kaira* lacks the white line on a black sternum as seen in the *M. labyrinthea* species group. Also, within the *M. foxi* species group, *M. daytona* is probably the most basal species because the ratios between patella-tibia and metatarsus-tarsus articles are the same as they are in *Kaira* (about 1.1:1); whereas in all other known *Metepeira* species the ratio is about 0.9:1. Thus, with *Kaira* as the outgroup, our results support the relatively basal origins of species in the *M. foxi* species group. However, since this group is defined by exclusively symplesiomorphic

characters, we cannot infer that it is monophyletic.

Nine unambiguous synapomorphies support the inclusion of *Z. atrica* within the Araneidae (Fig. 4). Forcing *Z. atrica* into the Tetragnathidae costs four additional steps. In addition, 1000 bootstrap replicates using PAUP support the araneid clade 76% of the time. Thus, our data disagree with Levi (1980) and others who believe that *Zygiella* is a tetragnathid.

However, we should mention that the monophyly of *Zygiella* is uncertain. On the one hand, the vacant sector in the orb web, the compact eye region, and the dorsoventrally flattened oval abdomen with its characteristic markings, seem to unite *Zygiella* species (Levi 1974). On the other hand, the inconsistency in the presence of a scape, terminal apophysis, paracymbium shape, tooth on the palpal endite, and seta on the palpal patella, put monophyly of the genus into question (Levy 1986). Levi (1974) argues that the remarkable diversity in *Zygiella* genitalia fails to break apart the genus because many inconsistent characters overlap one another. For example many species that lack a scape still share a derived ventral apophysis of the tegulum with other species that have a scape (Levi 1980). Thus, while it is still possible that *Zygiella* is paraphyletic, and while it is possible that some *Zygiella* species are, in fact, tetragnathids, our data argue that at least the type species for the genus, *Z. atrica*, appears to be an araneid.

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## SCHARFFIA, A REMARKABLE NEW GENUS OF SPIDERS FROM EAST AFRICA (ARANEAE, CYATHOLIPIDAE)

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**ABSTRACT.** The new genus *Scharffia* (Araneae, Cyatholipidae), comprising the new species *Scharffia chinja*, *Scharffia holmi*, *Scharffia nyasa* and *Scharffia rossi*, is described.

Discovered in southern Africa near the end of the last century (Simon 1894; Cambridge 1903), the Cyatholipidae comprise rich faunas in the cool-temperate southern latitudes of Africa (Griswold 1987) and Australasia (Forster 1988). They are typical denizens of the “Afromontane” forests (White 1978; Griswold 1991) of the mountains and Cape coasts of South Africa and, as is the case with many other animals and plants, their occurrence in the moist, montane forests making up the “Afromontane archipelago” in tropical Africa should come as no surprise. Cyatholipids have recently been described from Madagascar (Griswold 1997): herein I describe the first cyatholipids recorded from tropical Africa.

Most collection records suggest that *Scharffia* favor wet forests. They are common in montane forests (i.e., above 800 m elevation) and typically absent from nearby lowland forests (though at least *S. chinja* new species has been collected beneath 300 m elevation). *Scharffia rossi* new species was collected in dry savanna far from forest, and, like *Cyatholipus hirsutissimus* Simon 1894 and *Ulwembua denticulata* Griswold 1987 (Griswold 1987), indicates that the family is not entirely restricted to forests.

As is typical of cyatholipids, *Scharffia* hang beneath sheet webs (Figs. 2–4; Davies 1978; Forster 1988; Griswold et al. in press) and were rarely collected away from webs (e.g., in pitfalls or by sifting). The function of the elongate, annulate abdominal petiole (Fig. 1) is unknown; but, to the casual observer, it renders the spiders remarkably similar to ants. The awl-shaped abdomen of the *S. chinja* population at Mazumbai in the West Usambara Mountains of Tanzania (Fig. 19) makes them strikingly similar to *Cre-*

*matogaster* ants. Nevertheless, this resemblance is not enhanced by hanging beneath sheet webs, nor do spiders collected on beating sheets move like ants: mimicry is a doubtful explanation for their remarkable abdominal modification. The sclerotized petiole may function in carapace-abdomen stridulation, as recorded in the cyatholipid sister group Synotaxidae (Forster, Platnick & Coddington 1990; Griswold et al. in press).

### METHODS

Prior to examination with a Hitachi S-520 Scanning Electron Microscope all structures were critical point dried. Vulvae were cleaned by exposure to trypsin, bleached in 5% sodium hypochlorite (Chlorox<sup>®</sup>), stained with Chlorazol Black, and mounted in Hoyer's Medium for examination and photography. Examination was via Wild M5Apo and Leitz Ortholux II microscopes; and photography of vulvae was by an Olympus PM-10AK attached to the Leitz Ortholux II. Small structures were examined in temporary mounts as described in Coddington (1983).

Abbreviations are listed in Table 1. All measurements are in mm. For the key and diagnoses the ratio of the length of the palpal bulb (LPB)/length of the median lobe of the tegulum (MLT) is based on the measurements: LPB = distance from distal margin of the apical lobe (A) of the tegulum to the proximal-most extent of the embolic curve; MLT = distance from distal margin of the apical lobe (A) of the tegulum to the proximal margin of the median lobe. Specimens measured were chosen to encompass largest and smallest individuals.

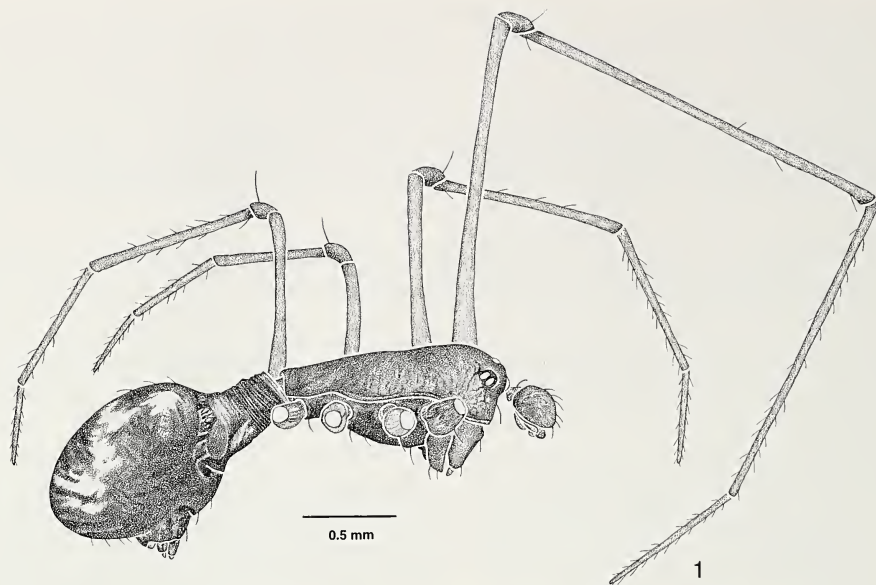


Figure 1.—*Scharffia rossi* new species, holotype male, lateral view.

## TAXONOMY

### Cyatholipidae Simon 1894

Cyatholipeae Simon 1894: 711, based on *Cyatholipus hirsutissimus* Simon 1894. Roewer 1942: 967.

Cyatholipinae, Wunderlich 1978: 33.

Teemenaaridae Davies 1978: 42, based on *Teemenaarus silvestris* Davies 1978.

Cyatholipidae Platnick 1979: 116. Brignoli 1983: 231. Griswold 1987: 501. Forster 1988: 7. Platnick 1989: 181. Platnick 1993: 172. Wunderlich 1993: 234.

**Diagnosis.**—Colulate, entelegyne araneoids that share with the Synotaxidae a cup-shaped paracymbium (Figs. 27, 35) and posteriorly broadly truncate sternum, and differing in having a retromedian cymbial process (Figs. 12, 27) and very broad posterior respiratory groove (Figs. 10, 21). For full description see Griswold (1987) and Forster (1988).

### *Scharffia* new genus

**Type species.**—*Scharffia chinja* new species.

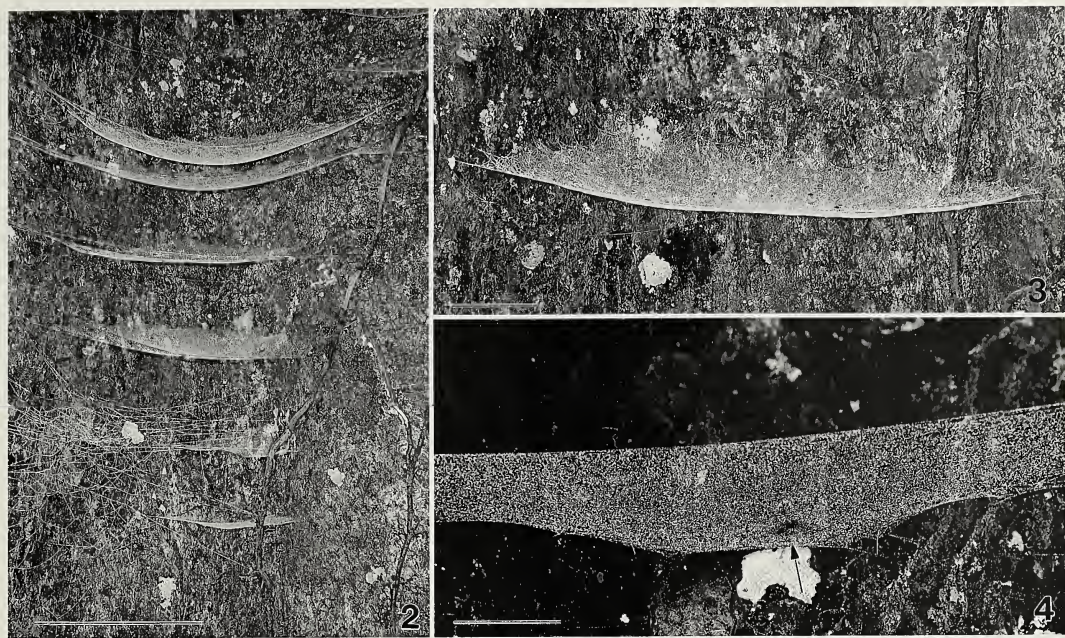
**Etymology.**—Named in honor of Nikolaj Scharff, Afromontane arachnologist and collector of many new and interesting Cyatholipidae; gender feminine.

**Note.**—*Scharffia* has been previously mentioned as “an undescribed genus occurring in montane forests from Malawi to Kenya” related to the Malagasy *Alaranea* (Griswold 1997, p. 82).

**Diagnosis.**—Distinguished from all Cyatholipidae by having the sternum elongate, prolonged between coxae IV, with length greater than  $1.15\times$  width (Figs. 8, 21, 36), and from all genera except *Alaranea* by having the anterior portion of abdomen of both sexes forming a sclerotized, annulate petiole, in most species elongate (Figs. 11, 16–22).

**Description.**—Total length 2.25–3.25. Carapace typically trapezoidal or diamond-shaped in dorsal view (Fig. 20), may be prolonged posteriorly (Fig. 32), length  $1.58\text{--}2.43\times$  width, posterior margin truncate, low, maximum height  $0.35\text{--}0.57\times$  width, texture rugose (Fig. 9); thoracic fovea typically shallow, diamond-shaped to indistinct; ocular area with PER width  $2.18\text{--}2.93\times$  OAL,  $2.25\text{--}2.80\times$  OQP, OQP  $0.87\text{--}1.20\times$  OQA; diameter AM  $1.09\text{--}1.87\times$  PM, distance PM-PL  $1.20\text{--}2.25\times$  PM diameter; clypeal height  $1.86\text{--}2.80\times$  AM diameter, cheliceral length  $1.35\text{--}2.54\times$  clypeal height; chelicerae unmodified or with small basal protuberance, promargin with four, retromargin with three teeth (Fig. 6). Sternum rugose to pustulate (Fig. 8), length  $1.15\text{--}1.58\times$  width, coxae surrounded by pleural and sternal sclerotizations (Figs. 1, 5, 8). Abdomen oval to triangular, with short, slender setae, bases of anterior setae unmodified, sclerotized from epigastric furrow to and surrounding pedicel to form short-to-long annulate petiole (Figs. 11,





Figures 2–4.—Webs of *Scharffia chinja* new species, from Amani. 2, Webs on tree buttress (Scale bar = 10.0 cm); 3, Web, close up (Scale bar = 5.0 cm); 4, Underside of web with spider (arrow) (Scale bar = 1.0 cm).

26), spinnerets surrounded by yellow-brown sclerotization with dark radial streaks (Figs. 21, 36). Legs unmodified, long (Figs. 1, 18) to extremely long (Fig. 43), ratio 1-2-4-3, female femur I length 2.42–4.67× carapace width, male 2.51–9.48. Male palpus with retrolateral cymbial process (RMP) pointing ventrad (Figs. 12, 27), smaller than paracymbium (PC); palpal bulb (Figs. 14, 27–29) with dentate median lobe (MLT), apex (A) a small, smooth to pustulate lobe; conductor (C) median, longitudinal, simple (Figs. 28, 29, 57) or with accessory process (Figs. 14, 52), smooth; embolus (E) thick, making simple curve, origin apical between 10-11 o'clock, ridged; parembolic process (PP)

present (Figs. 14, 15, 53) or absent (Figs. 28, 56), thick and fleshy with a median attenuate projection, lacking teeth, with or without pustules; sperm duct with curlicue near embolic base. Epigynum (Figs. 23–26) with scape (S) and median hood (MH) with slender septum between copulatory openings (CO), atrial furrows (AT) extending behind scape. Vulva (Figs. 37–40) with sclerotized, simple, narrow to hemispherical lateral afferent duct (AD), fertilization duct (FD) posterior to spermathecal head (HS).

**Composition.**—Four species.

**Distribution.**—East Africa from Malawi to Kenya (Fig. 58).

KEY TO SPECIES OF *SCHARFFIA*

- 1 Abdomen with petiole length greater than 0.24 of carapace length (Figs. 1, 18, 20) ..... 2
- Abdomen with petiole length less than 0.17 of carapace length (Figs. 41–43) ..... *nyasa*
- 2(1) Posterior portion of carapace elongate, forming parallel-sided neck, carapace length greater than twice width (Figs. 1, 32); embolus without parembolic process (Figs. 30, 34); conductor simple; epigynal scape twice as long as wide (Fig. 33) ..... 3
- Carapace diamond-shaped in dorsal view (Figs. 19, 20), posterior portion tapering, carapace length less than twice width; embolus with parembolic process (Fig. 44); conductor double; epigynal scape much wider than long (Fig. 46) ..... *chinja*
- 3(2) Length palpal bulb less than 2× that of the median lobe of the tegulum (MLT), tegulum nearly hidden between MLT and embolus (Figs. 30, 56). ..... *rossi*
- Length palpal bulb greater than 2.5× MLT, tegulum clearly visible between MLT and embolus (Figs. 28, 34) ..... *holmi*



Table 1.—List of anatomical abbreviations used in the text and figures.

A	apical lobe of tegulum
AD	vulval afferent duct
AER	anterior eye row
AL	anterior lateral eyes
AM	anterior median eyes
AT	epigynal atrium
C	conductor
CB	cymbium
CO	copulatory opening
E	embolus
EF	epigastric furrow
FD	fertilization duct
HS	spermathecal head
LPB	length palpal bulb
MH	epigynal median hood
ML	epigynal median lobe
MLT	median lobe of tegulum
MS	epigynal median septum
OAL	ocular area length
OQA	ocular quadrangle, anterior
OQP	ocular quadrangle, poseterior
PC	paracymbium
PER	posterior eye row
PL	posterior lateral eyes
PM	posterior median eyes
PP	parembolic process
RMP	retromedian cymbial process
S	epigynal scape
ST	subtegulum
T	tegulum
TL	ventromedian tegular lobe

*Scharffia chinja* new species

(Figs. 2–23, 25, 38, 40, 44–46, 58)

**Types.**—Male holotype and female paratype from intermediate rain forest at Uzungwa Scarp Forest Reserve above Chita village, elev. 1050 m, Uzungwa Mts., Iringa Region, Tanzania, 5 November 1984 (N. Scharff) (ZMUC).

**Etymology.**—The specific epithet is an arbitrary combination of letters.

**Diagnosis.**—Distinguished from *nyasa* new species by having the abdominal petiole greater than 0.24 carapace length (Figs. 18, 20); males distinguished from *rossi* new species and *holmi* new species by having a parembolic process and double conductor (Figs. 44, 45); females distinguished from *holmi* by having a broad scape (Fig. 46) and hemispherical afferent ducts (Figs. 38, 40).

**Description.**—*Male (holotype):* Total

length 2.64. Carapace, clypeus, chelicerae, sternum, labium, and palpal coxae dark red-brown, unmarked except for dusky maculations on clypeus; palpi dark yellow-brown, unmarked; coxae, trochanters, and legs yellow-brown, unmarked except for subbasal brown annulus on femur IV; abdomen dark gray, dorsum with narrow longitudinal and broad transverse white markings forming cross. Carapace 1.21 long, 0.61 wide, 0.29 high, prolonged posteriorly to meet abdominal petiole; PER 0.38 wide, AER 0.37 wide, OAL 0.17; ratio AM:AL:PM:PL, 1.6:1.2:1.0:1.2, PM diameter 0.05. Clypeus 0.18 high, chelicerae 0.26 long. Sternum 0.58 long, 0.47 wide; labium 0.10 long, 0.16 wide; palpal coxae 0.18 long, 0.14 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I: 2.64 + 0.25 + 2.23 + 2.13 + 0.91 = [8.13]; II: 1.81 + 0.23 + 1.57 + 1.49 + 0.72 = [5.82]; III: 0.87 + 0.17 + 0.64 + 0.62 + 0.40 = [2.70]; IV: 1.32 + 0.19 + 1.06 + 0.87 + 0.42 = [3.80]; Palp: 0.26 + 0.10 + 0.08 + (absent) + 0.26 = [0.70]. Palp (Figs. 12–15, 44, 45) with RMP narrowly triangular, PC narrow, deeply concave in lateral view; tegulum apex pustulate, MLT large, convex, dentation restricted to narrow longitudinal band; C large, with small narrow secondary process; PP present, lacking pustules.

*Variation:* ( $n = 7$ ). Total length 2.34–2.89; ratios of carapace length/width 1.74–2.00, height/width 0.35–0.52, PER/OQP 2.37–2.64, PER/OAL 2.19–2.80, OQP/OQA 0.87–1.07, diameter AM 1.18–1.60 times PM; ratios of clypeal height/AM diameter 2.12–2.61, chelicer length/clypeal height 1.35–1.87; ratio of sternum length/width 1.15–1.46; ratio of femur I length/carapace width 4.00–5.01. The shape of the soft part of the abdomen ranges from nearly round (Figs. 17, 22) to triangular (Figs. 16, 18, 20) to heart- to awl-shaped (Fig. 19: dorsal view of Mazumbai specimen). Markings also vary greatly: the dorsum may be all dark, have lateral light spots (Fig. 17) or a narrow to broad transverse median band (Fig. 22); a narrow to broad longitudinal median band may be present anteriorly (Fig. 19), separate from transverse band (Fig. 20) or connected to it to form a light cross (Fig. 16).

*Female (paratype):* Total length 2.58. Markings as in male except white markings of abdomen not forming cross, longitudinal dorsal mark attenuate anteriorly, with anterolat-



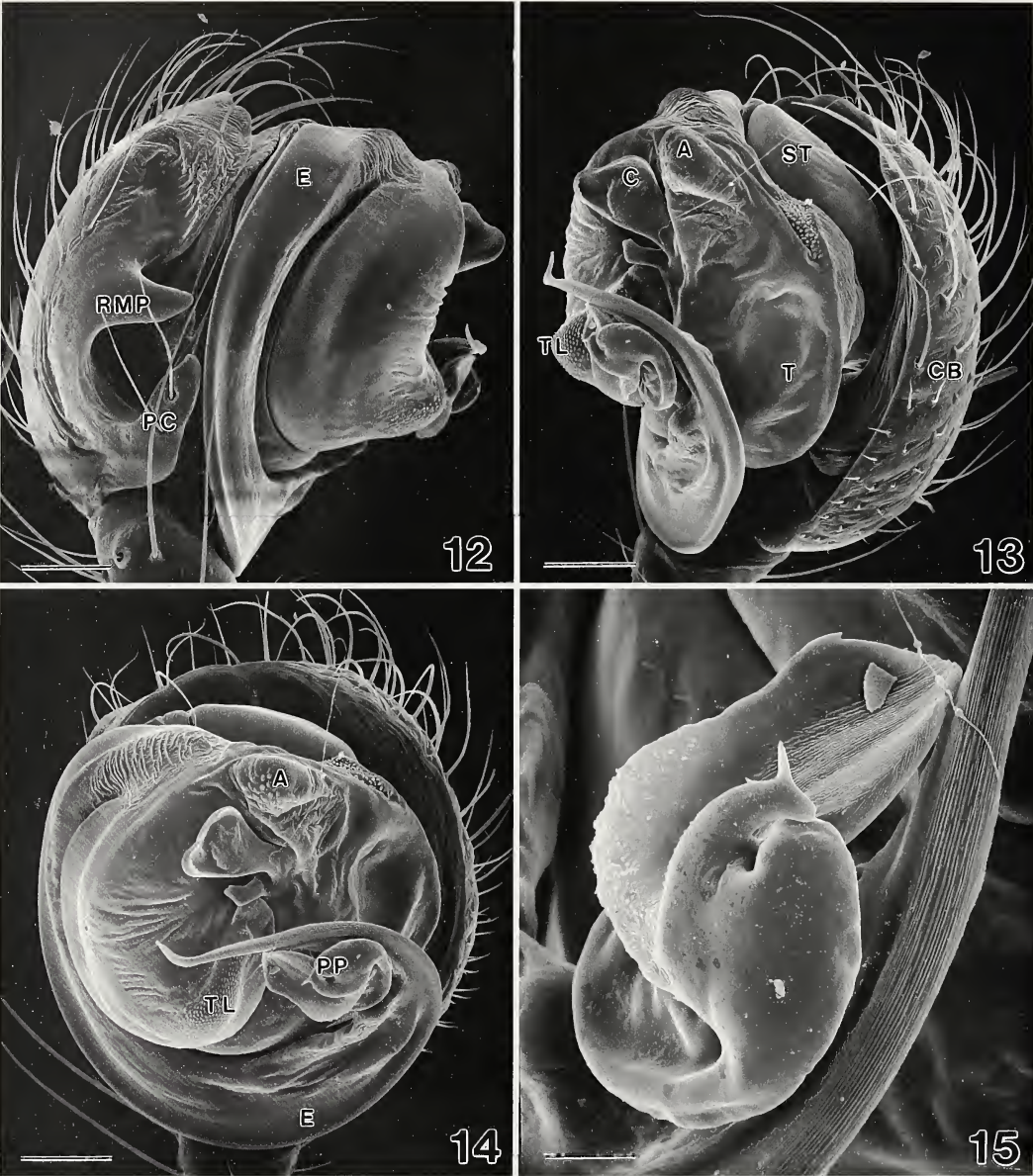


Figures 5–11.—*Scharffia chinja* new species, female, from Uzungwa. 5, Carapace, lateral; 6, Mouthparts, ventral; 7, Face; 8, Sternum and petiole, ventral; 9, Carapace, dorsal; 10, Spinnerets and posterior spiracle (arrows); 11, Abdominal petiole, lateral. (Scale bars for Figs. 5–8, 11 = 100  $\mu$ m; Fig. 9, 250  $\mu$ m; and Fig. 10, 50  $\mu$ m.)

eral faint white spot and median lateral transverse band. Structure as in male; carapace 1.17 long, 0.58 wide, 0.28 high; PER 0.39 wide, AER 0.38 wide, OAL 0.17; ratio AM:AL:PM:PL, 1.6:1.2:1.0:1.4, PM diameter

0.05. Clypeus 0.17 high, chelicerae 0.33 long. Sternum 0.67 long, 0.44 wide; labium 0.11 long, 0.14 wide; palpal coxae 0.20 long, 0.16 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I: 1.72



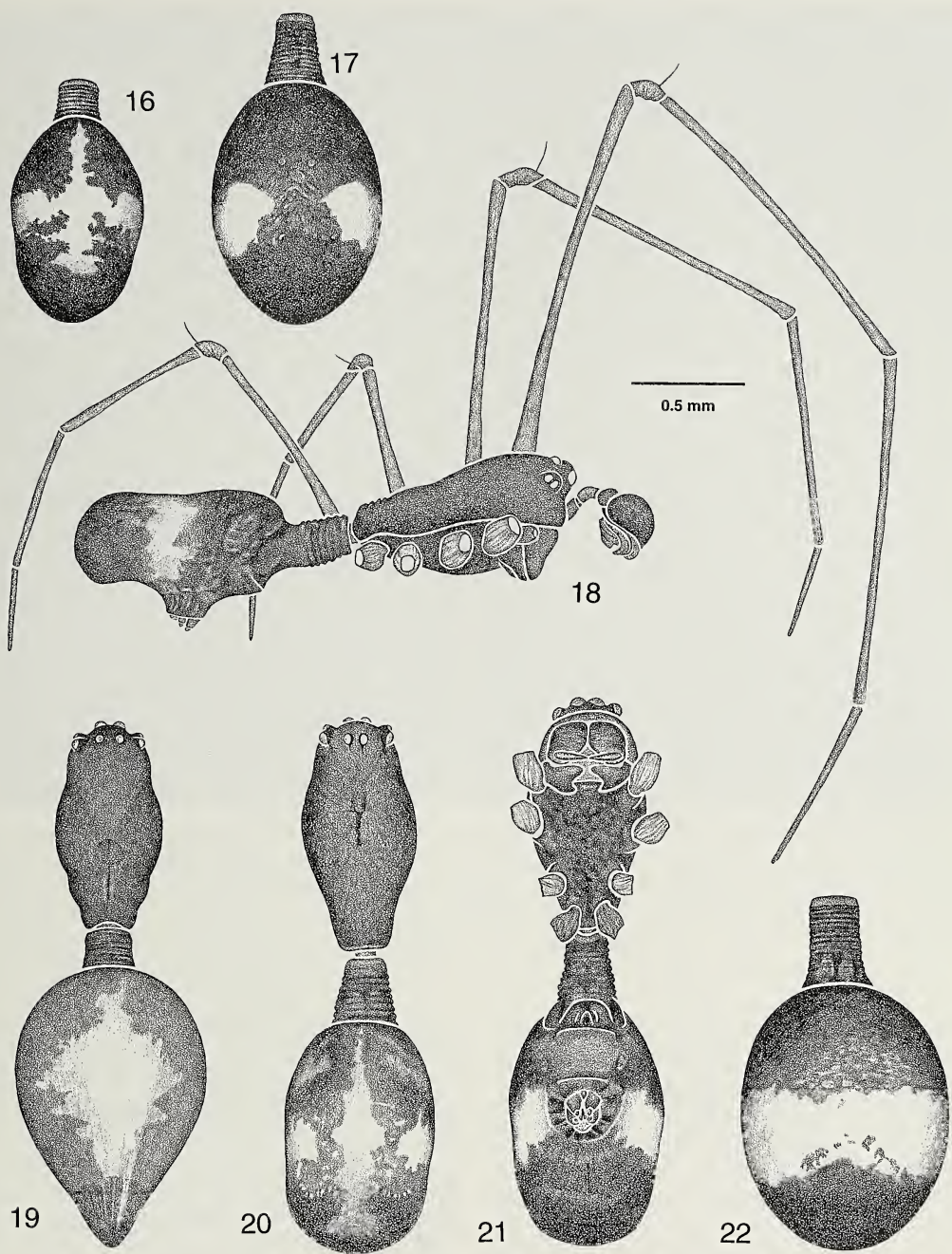


Figures 12–15.—*Scharffia chinja* new species, from Amani, right male palpus. 12, Retrolateral; 13, Prolateral; 14, Ventral; 15, Parembolic process. A = apical lobe of tegulum, C = conductor, CB = cymbium, E = embolus, PP = parembolic process, RMP = retromedian cymbial process, ST = subtegulum, T = tegulum, TL = ventromedian tegular lobe. (Scale bars for Figs. 12–14 = 60  $\mu$ m, Fig. 15 = 15  $\mu$ m.)

+ 0.23 + 1.55 + 1.40 + 0.74 = [5.64]; II: 1.28 + 0.21 + 1.06 + 0.96 + 0.57 = [4.08]; III: 0.70 + 0.15 + 0.53 + 0.47 + 0.34 = [2.19]; IV: 1.17 + 0.19 + 0.89 + 0.70 + 0.38 = [3.33]; Palp: 0.24 + 0.07 + 0.13 + (absent) + 0.27 = [0.71]. Epigynum as in Figs. 23, 25, 46, S convex; vulva as in Fig. 40, AD anterior, larger than or equal to HS.

*Variation:* (n = 7). Total length 2.28–3.19; ratios of carapace length/width 1.81–2.07, height/width 0.49–0.56, PER/OQP 2.28–2.80, PER/OAL 2.31–2.93, OQP/OQA 0.94–1.20, diameter AM/PM diameter 1.27–1.60; clypeal height 1.86–2.80 times AM diameter, chelicer length 1.67–2.54 times clypeal height; ratio of sternum length/width 1.14–1.58; ratio



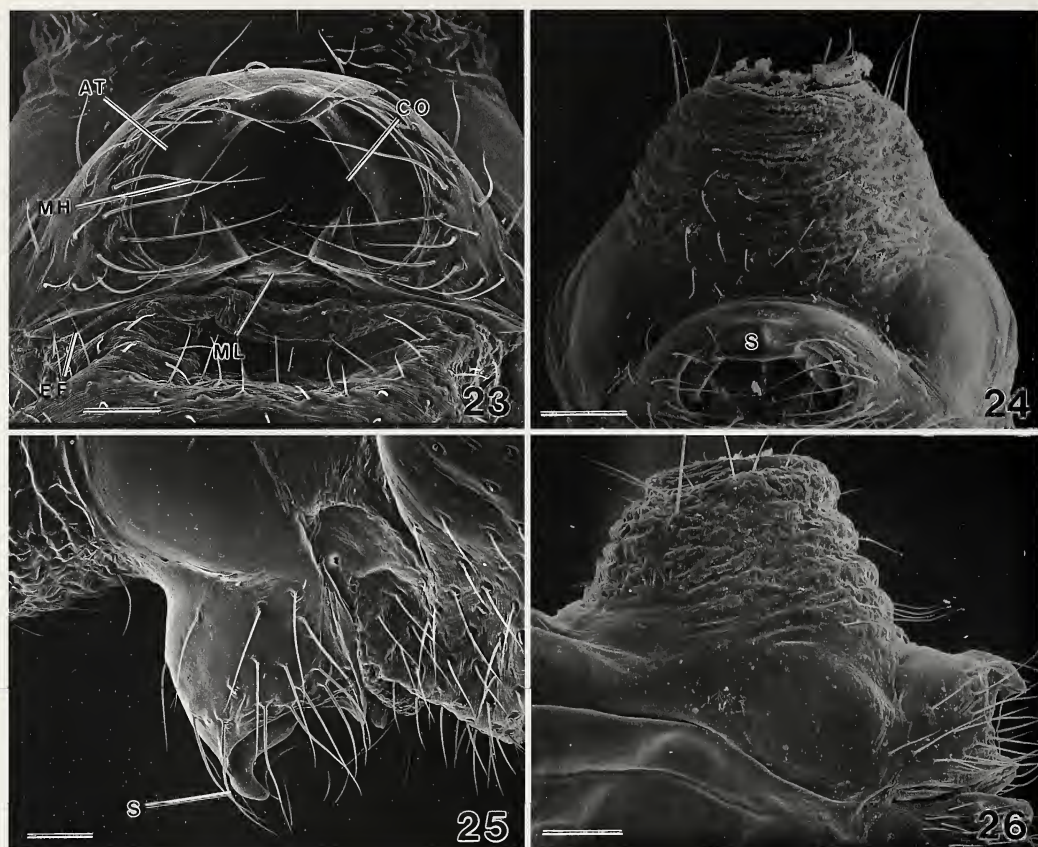


Figures 16–22.—*Scharffia chinja* new species. 16, 17, 22, Females, from Amani, dorsal view of abdomen; 18, Male, from from Uzungwa, lateral view; 19, Female, from Mazumbai, dorsal; 20, 21, Female, from Uzungwa; 20, Dorsal; 21, Ventral.

of length femur I/carapace width 2.42–3.26. Abdominal shape and markings vary as in male (Figs. 16, 17, 19–22). AD larger than (Fig. 38) or equal to (Fig. 40) HS.

**Natural history.**—The spiders hang be-

neath sheet webs in shaded areas in forest (Figs. 2–4). In addition to juveniles and adult females, adult males may be found in intact webs, and both sexes may occur in the same web.



Figures 23–26.—*Scharffia* female epigynum and abdominal petiole. 23, 24, Ventral; 25, 26, Lateral; 23, 25, *Scharffia chinja* new species, from Uzungwa; 24, 26, *Scharffia nyasa* new species. AT = epigynal atrium, CO = copulatory opening, EF = epigastric furrow, MH = epigynal median lobe, ML = epigynal median hood, S = epigynal scape. (Scale bars for Figs. 23, 25 = 50  $\mu$ m, Fig. 24 = 100  $\mu$ m, Fig. 26 = 75  $\mu$ m.)

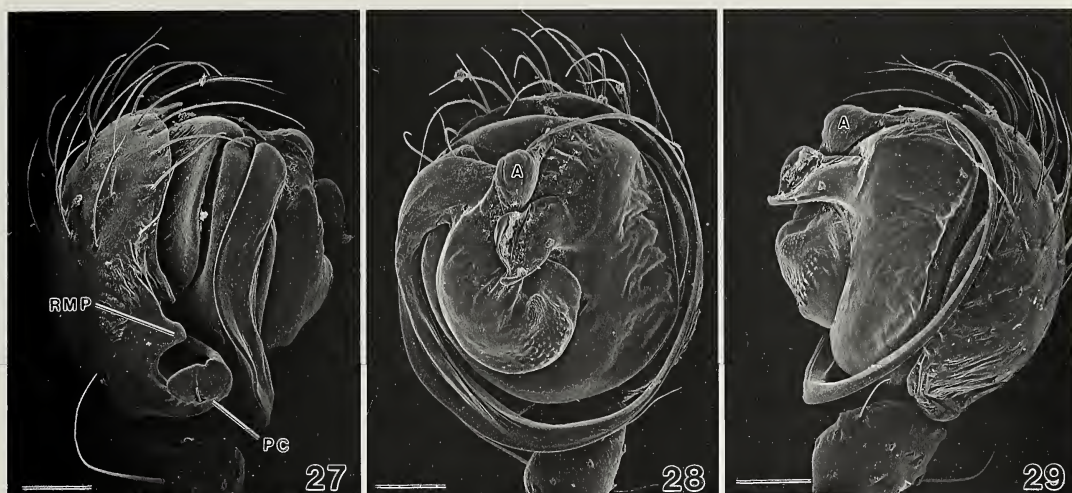
**Distribution.**—Eastern Arc mountains and nearby lowlands of Tanzania (Fig. 58).

**Additional material examined: TANZANIA:**

**Coast Region:** Kisarawe District: Kazimzumbwe Forest Reserve, 20 km SW Dar-es-Salaam, 6°57'S, 39°03'E, elev. 120–280 m, January–February 1991, 1♂2♀ (Frontier Tanzania Expedition) (ZMUC). **Tanga Region:** East Usambara Mts. (all C. Griswold, D. Ubick, & N. Scharff, 1995, CAS and ZMUC): Amani, 5°05'S, 38°38'E, elev. 950 m, 27 October–9 November, 50♂63♀; Mbomole Hill, 5°05'S, 38°37'E, elev. 1000 m, 5–8 November, 2♂15♀; Kwamkoro Forest Reserve, 5°10'S, 38°35'E, elev. 950 m, 6 November, 8♂13♀; Sangarawe Forest, 38°35'E, 5°06'S, elev. 990 m, 5–6 November, 1♂3♀; Segoma Forest Reserve, 4°58'S, 38°45'E, primary rain forest, 17 February 1987, S. Mahunka, T. Pöcs, & A. Zicsi, 1♀ (HMNH); West Usambara Mts., Mazumbai, 4°49'S, 38°30'E, elev. 1400–1600 m, 10–20 November 1995 (C. Griswold, D. Ubick,

& N. Scharff), 15♂45♀ (CAS, ZMUC); 1 August 1980, M. Stoltze and N. Scharff, 1♂1♀ (ZMUC). **Morogoro Region:** Uzungwa Mts.: Mwanihana Forest Reserve (all N. Scharff, 1984, ZMUC): elev. 500–700 m, 7–16 September, 1♂; elev. 500–600 m, 11–14 September, pitfalls, 1♀; elev. 700 m, 7 September, litter, 1♀; elev. 1400 m, 27 September, 1♀; elev. 1650 m, 25–29 September, litter, 1♀; elev. 1800–1850 m, 28–29 September, netted, 1♀. Mwanihana Forest Reserve above Sanje (all M. Stoltze & N. Scharff, ZMUC): elev. 600 m, 3 August 1982, 1♀; elev. 700 m, 10 September 1984, 1♀; 12 September 1984, netted, 2♂; elev. 750 m, 1 August 1981, 5♂; elev. 1000 m, 1 August 1981, 2♀; 1 August 1982, 1♂3♀; elev. 1250 m, 25 July 1982, 1♂1♀; elev. 1650 m, 18 August 1982, litter, 1♂2♀; pitfall, 3♀. **Iringa Region:** Uzungwa Scarp Forest Reserve above Chita village (all N. Scharff, 1984, ZMUC): elev. 1050 m, 26 October, litter, 1♀; elev. 1300 m, 2–6 November, 1♀; elev. 1300 m, 3





Figures 27–29.—*Scharffia holmi* new species, holotype male, right palpus. 27, Retrolateral; 28, Ventral; 29, Prolateral. A = apical lobe of tegulum, PC = paracymbium, RMP = retromedian cymbial process. (Scale bars for Figs. 27–29 = 50  $\mu$ m.)

November, litter, 1 ♀; elev. 1400 m, 4 November, netted, 1 ♀; 10 November, netted, 2 ♀; elev. 1500 m, 9 November, litter, 1 ♂; 11 November, netted, 1 ♂ 2 ♀; elev. 1600 m, 10 November, 1 ♀; elev. 1650 m, 13 November, netted, 1 ♂ 1 ♀. *Mbeya Region*: Mt. Rungwe SW, elev. 1900 m, 20 August 1984, M. Stoltze & N. Scharff, 1 ♂ (ZMUC).

*Scharffia holmi* new species  
(Figs. 27–29, 32–36, 39, 58)

**Types.**—Male holotype and two female paratypes from Mount Elgon, Kenya, elev. 2300 m, 23 December 1937, Å. Holm (UuzM).

**Etymology.**—Named in honor of Åke Holm, collector of the type and student of African montane spiders.

**Diagnosis.**—Distinguished from all *Scharffia* except *S. rossi* new species by lacking a parembolic process (Figs. 28, 34), having a simple conductor, and having the cephalothorax prolonged posteriorly to form a parallel-sided neck (Fig. 32), and from *rossi* new species by having the length of the palpal bulb greater than  $2.5\times$  length of median lobe of tegulum (MLT), with the tegulum clearly visible between MLT and embolus (Figs. 28, 34). The epigynum is unique in *Scharffia* in having a narrow scape (Fig. 33) twice as long as wide, and the vulva unusual in Cyatholipidae in having a lateral afferent duct that is smaller than the spermethecal head (Fig. 39).

**Description.**—*Male (holotype)*: Total

length 2.40. Carapace, chelicerae, palpal coxae, labium and sternum dark red-brown, unmarked except for dusky maculations along lateral margin of carapace and forming short longitudinal band antieriad of thoracic foveae; ocular area dark gray surrounding AM and between AM and AL, clypeus dark gray in center from beneath AM to oral margin; coxae, trochanters and legs yellow-white, unmarked except for faint dark mark at base of femur IV; palpi gray-brown, unmarked; abdomen dark gray, dorsum with diffuse longitudinal dark spot in center surrounded by paler cuticle. Carapace 1.15 long, 0.54 wide, 0.23 high, greatly prolonged posteriorly to form narrow neck meeting abdomen; PER 0.35 wide, AER 0.34 wide, OAL 0.14; ratio AM:AL:PM:PL, 1.5:1.0:1.12:1.25, PM diameter 0.05. Clypeus 0.15 high, chelicerae 0.25 long. Sternum 0.70 long, 0.46 wide; labium 0.09 long, 0.13 wide; palpal coxae 0.16 long, 0.10 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $1.36 + 0.19 + 1.28 + 1.23 + 0.66 = [4.72]$ ; II:  $1.02 + 0.17 + 0.83 + 0.76 + 0.49 = [3.25]$ ; III:  $0.66 + 0.15 + 0.47 + 0.47 + 0.34 = [2.09]$ ; IV:  $0.70 + 0.17 + 0.72 + 0.59 + 0.38 = [2.56]$ ; Palp:  $0.23 + 0.07 + 0.07 + (\text{absent}) + 0.22 = [0.59]$ . Palp (Figs. 27–29, 34, 35) with RMP short, blunt, PC broad in lateral view; tegulum apex low, smooth, MLT small and denticulate over median oval area, tegulum exposed beneath; C simple, single; PP absent.

*Female (paratype)*: Total length 2.47. Markings and structure as in male (Figs. 32, 36). Carapace 1.20 long, 0.54 wide, 0.26 high; PER 0.35 wide, AER 0.34 wide, OAL 0.14; ratio AM:AL:PM:PL, 1.5:1.37:1.0:1.5, PM diameter 0.04. Clypeus 0.11 high, chelicerae 0.27 long. Sternum 0.69 long, 0.45 wide; labium 0.10 long, 0.14 wide; palpal coxae 0.19 long, 0.13 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $1.38 + 0.21 + 1.21 + 1.15 +$  (missing) = [?]; II:  $1.02 + 0.18 + 0.85 + 0.76 + 0.49 = [3.28]$ ; III:  $0.70 + 0.17 + 0.47 + 0.45 + 0.38 = [2.17]$ ; IV:  $0.98 + 0.16 + 0.79 + 0.66 + 0.36 = [2.95]$ ; Palp:  $0.21 + 0.08 + 0.10 +$  (absent)  $+ 0.23 = [0.62]$ . Epigynum as in Fig. 33, S narrow; vulva as in Fig. 39, AD lateral, smaller than HS.

*Variation*: ( $n = 2$ ). Total length 2.47–2.72; ratios of carapace length/width 2.25–2.43, height/width 0.49–0.57, PER/OQP 2.36–2.44, PER/OAL 2.54–2.60, OQP/OQA 0.93–0.94, diameter AM/PM 1.50–1.87; clypeal height 2.36–2.44 times AM diameter, cheliceral length 2.06–2.36 times clypeal height; ratio of sternum length/width 1.45–1.53; ratio of length femur I/carapace width 2.55–3.03.

**Natural history**.—Unknown.

**Distribution**.—Known only from the type locality (Fig. 58).

**Material examined**.—Only the type specimens.

### *Scharffia nyasa* new species

(Figs. 24, 26, 37, 41–43, 47–53, 58)

**Types**.—Male holotype and female paratype from Widdringtonia evergreen forest at 2000 m on Lichenya Plateau on Mt. Mulanje, Malawi, 7 November 1981, R. Jocqué (MRAC 156.180).

**Etymology**.—An old name for Malawi.

**Diagnosis**.—Distinguished from all other *Scharffia* by having the petiole short, length less than 0.17 carapace length (Figs. 24, 41–43); also leg I extremely long (Fig. 43), femur I of female greater than 3.5, that of male greater than 5.4 times carapace width.

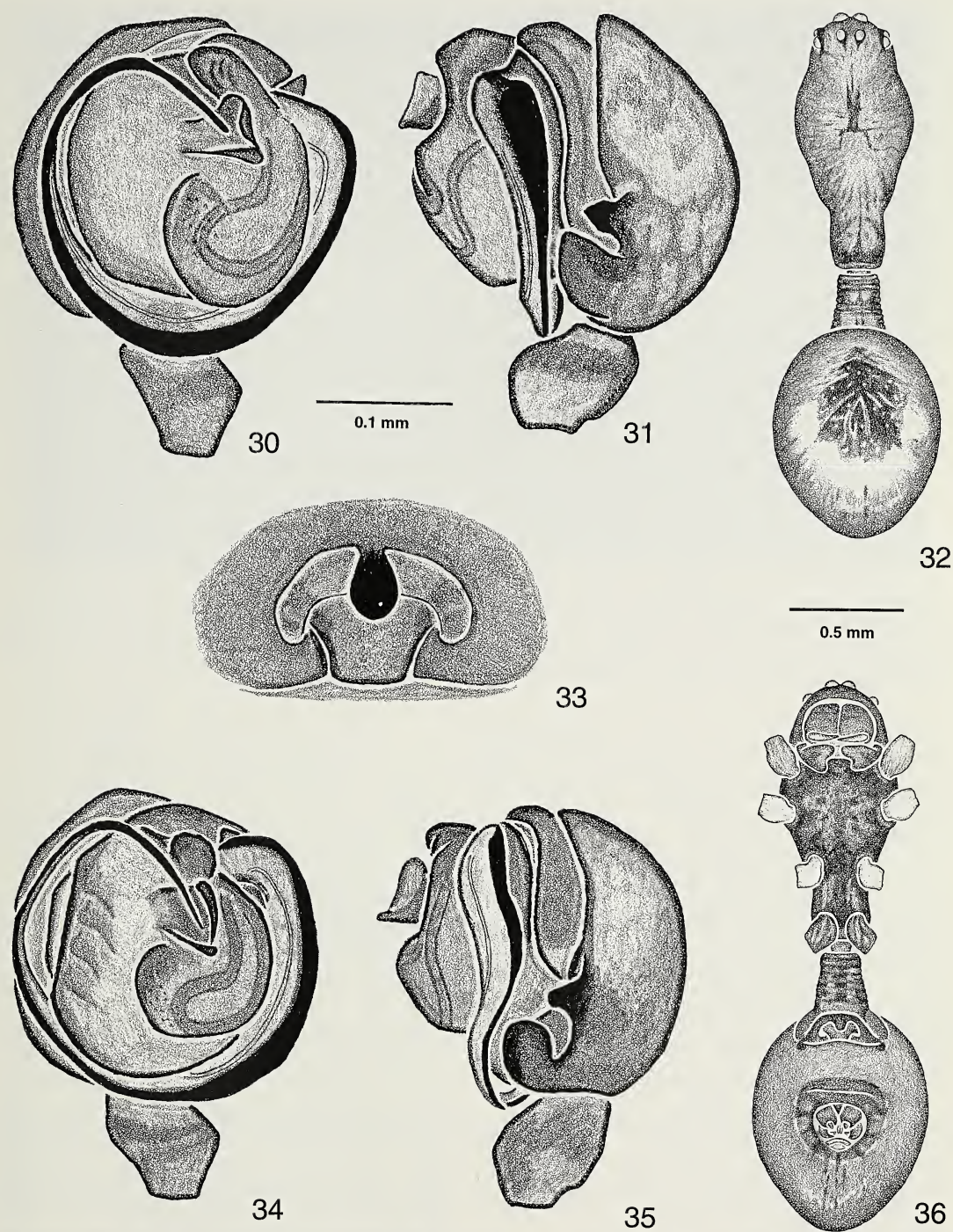
**Description**.—*Male (holotype)*: Total length 2.49. Carapace, palpal coxae, labium and sternum dusky red-brown, chelicerae dark yellow-brown, unmarked except for maculations along margin of carapace and anteriad of thoracic fovea; coxae, trochanters and bases of legs yellow-white, legs shading to yellow-

brown distally on femora to tarsi, unmarked except segments lighter at joints, palpi yellow-gray, cymbium dark red-brown; abdomen with dorsum black with central longitudinal light band, sides white shading to gray ventrally (Fig. 43). Carapace 0.98 long, 0.62 wide, 0.26 high, not prolonged posteriorly; PER 0.34 wide, AER 0.31 wide, OAL 0.15; ratio AM:AL:PM:PL, 1.2:1.0:1.0:1.1, PM diameter 0.05. Clypeus 0.15 high, chelicerae 0.29 long. Sternum 0.53 long, 0.45 wide; labium 0.10 long, 0.15 wide; palpal coxae 0.18 long, 0.14 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $3.40 + 0.23 + 3.23 + 3.57 + 1.21 = [11.64]$ ; II:  $1.55 + 0.19 + 1.34 + 1.15 + 0.66 = [4.89]$ ; III:  $0.83 + 0.17 + 0.62 + 0.57 + 0.40 = [2.59]$ ; IV:  $1.38 + 0.19 + 1.06 + 0.85 + 0.47 = [3.95]$ ; Palp:  $0.24 + 0.10 + 0.08 +$  (absent)  $+ 0.28 = [0.70]$ . Palp (Figs. 48–53) with RMP broadly triangular, PC narrow, sharply angled in lateral view; tegulum apex raised, pustulate, MLT large, with produced transverse denticulate ridge; C narrow at base, smooth, with small, narrow secondary process; PP present, pustulate.

*Variation*: ( $n = 5$ ). Total length 2.49–3.23; ratios of carapace length/width 1.58–1.73, height/width 0.40–0.48, PER/OQP 2.28–2.71, PER/OAL 2.22–2.29, OQP/OQA 0.93–1.08, diameter AM/PM 1.09–1.50; clypeal height 2.28–2.71 times AM diameter, cheliceral length 1.72–2.00 times clypeal height; ratio of sternum length/width 1.15–1.23; ratio of length femur I/carapace width 5.42–9.48 (Fig. 43).

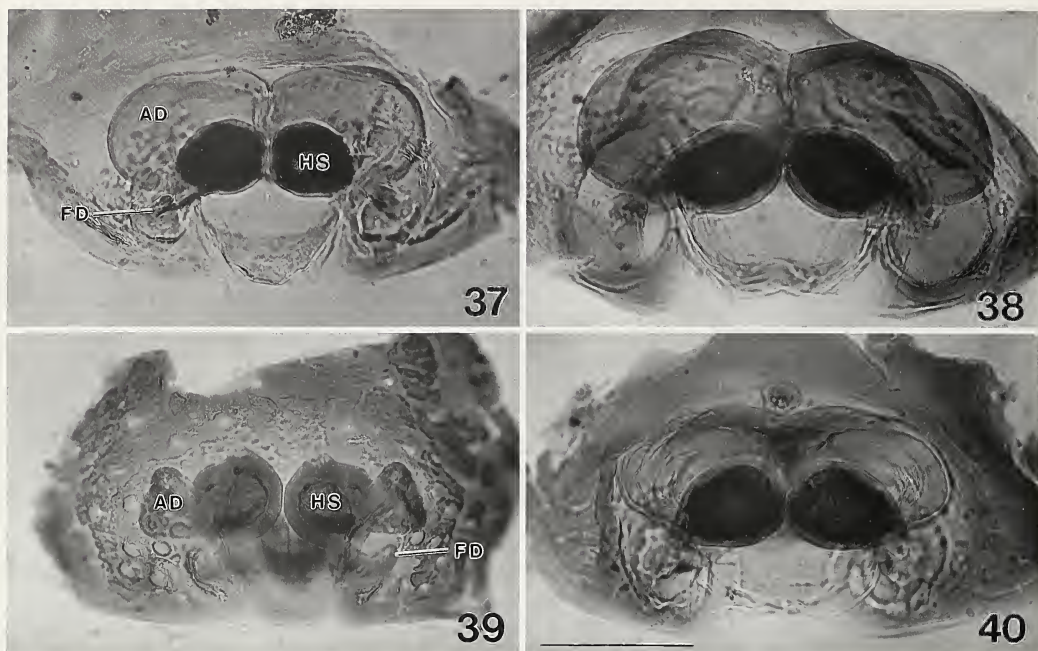
*Female (paratype)*: Total length 2.68. Markings and structure as in male except abdomen with dorsum dark gray enclosing long median and short anterolateral longitudinal white bands, sides white, venter yellow-gray (Figs. 41–42). Carapace 1.00 long, 0.57 wide, 0.26 high; PER 0.36 wide, AER 0.35 wide, OAL 0.15; ratio AM:AL:PM:PL, 1.3:1.1:1.0:1.1, PM diameter 0.05. Clypeus 0.11 high, chelicerae 0.28 long. Sternum 0.55 long, 0.44 wide; labium 0.10 long, 0.17 wide; palpal coxae 0.17 long, 0.13 wide. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [Total]): I:  $2.68 + 0.25 + 2.45 + 2.51 + 1.02 = [8.91]$ ; II:  $1.51 + 0.21 + 1.19 + 1.06 + 0.62 = [4.58]$ ; III:  $0.81 + 0.17 + 0.59 + 0.57 + 0.38 = [2.52]$ ; IV:  $1.34 + 0.19 + 1.00 + 0.87 + 0.45 = [3.95]$ ; Palp:  $0.21 +$





Figures 30–36.—*Scharffia*. 30, 31, *Scharffia rossi* new species, holotype male, left male palpus; 30, Ventral; 31, Retrolateral; 32–36, *Scharffia holmi* new species. 32, 33, 36, Paratype female; 32, Dorsal; 33, Epigynum, ventral; 36, Ventral; 34, 35, Holotype male, left male palpus; 34, Ventral; 35, Retrolateral. (Left scale bar for Figs. 30, 31, 33–35, right scale bar for Figs. 32, 36.)





Figures 37–40.—*Scharffia*, cleared female vulvae, dorsal view. 37, *Scharffia nyasa* new species; 38, *Scharffia chinja* new species, from Kazimzumbwe; 39, *Scharffia holmi* new species, paratype; 40, *Scharffia chinja* new species, from Uzungwa. AD = vulval afferent duct, FD = fertilization duct, HS = spermathecal head. (Scale bar (Fig. 40, applies to all) = 0.1 mm.)

$0.08 + 0.11 + (\text{absent}) + 0.27 = [0.67]$ . Epigynum as in Figs. 24, 26, 47, S broad and truncate; vulva as in Fig. 37, AD anterior, larger than HS.

**Variation:** ( $n = 4$ ). Total length 2.68–3.00; ratios of carapace length/width 1.65–1.76, height/width 0.38–0.46, PER/OQP 2.40–2.46, PER/OAL 2.25–2.43, OQP/OQA 0.93–1.16, diameter AM/PM 1.20–1.40; clypeal height 2.40–2.46 times AM diameter, cheliceral length 2.00–2.45 times clypeal height; ratio of sternum length/width 1.19–1.25; ratio of length femur I/carapace width 3.67–4.67.

**Natural history.**—Data on collection labels indicate occurrence in montane forest, where specimens were collected in litter and by sweeping.

**Distribution.**—Known only from the type locality (Fig. 58).

**Additional material examined.**—MALAWI: Mt. Mlanje (all R. Jocqué, 1981, MRAC): Thuchila Hut, Nambiti stream, elev. 2000 m, 11 November, 1♂1♀; Lichenya Plateau, *Widdringtonia* evergreen forest, elev. 2000 m, 4 November, 3♂2♀, 4–6 November, 1♀, 5 November, 1♀, 7 November, 1♀, 19 November, 1♂3♀, 21 November, 8♂30♀.

*Scharffia rossi* new species  
(Figs. 1, 30, 31, 54–58)

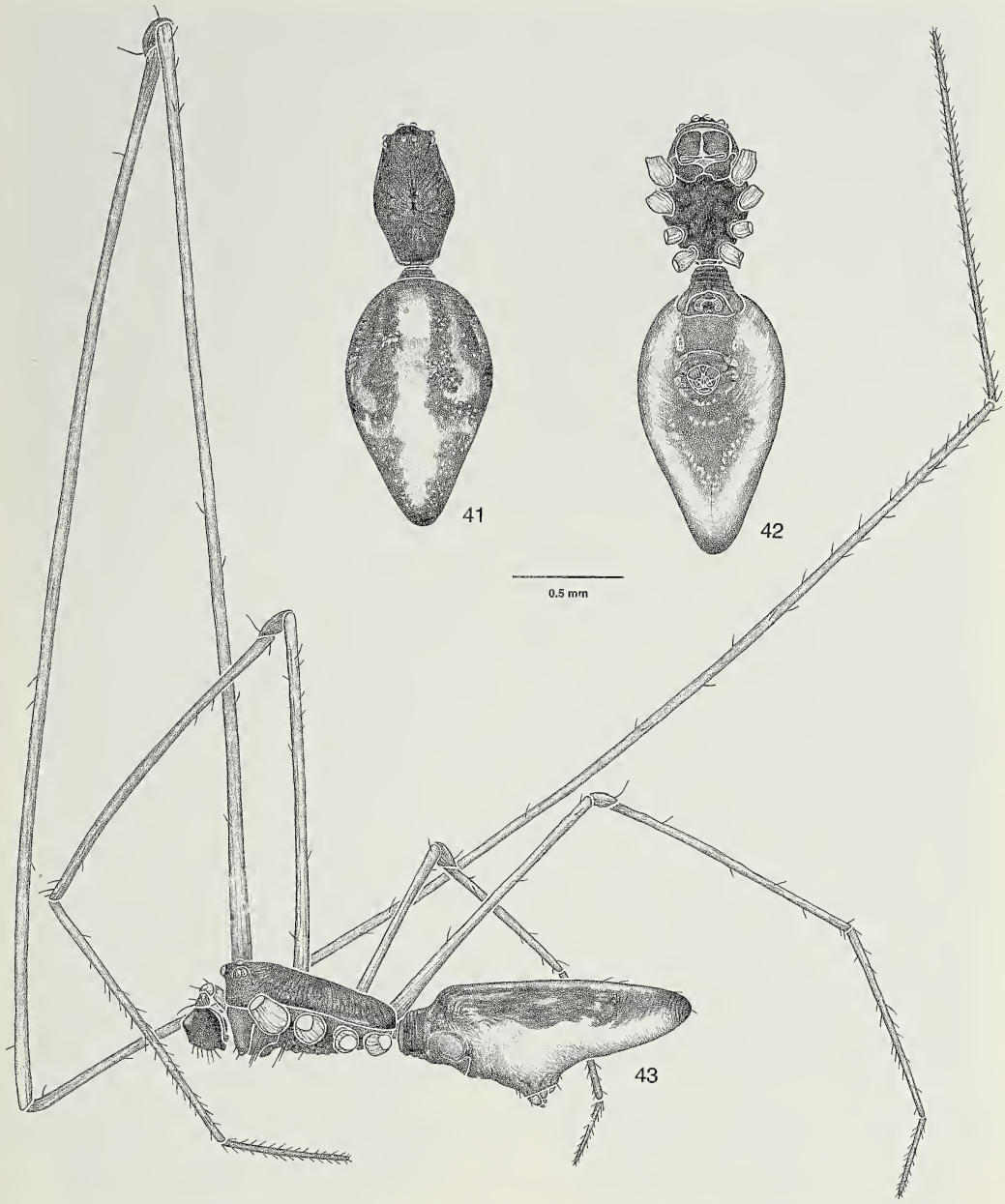
**Type.**—Male holotype from 1750 m at Naabi, Serengeti Plain, Tanzania, 25 October 1957, E. Ross and R. Leech (CAS).

**Etymology.**—In honor of Edward S. Ross, collector of this and many other new and interesting African arthropods.

**Diagnosis.**—Distinguished from all *Scharffia* except *S. holmi* new species by lacking a parembolic process, having a simple conductor (Fig. 57), and having the carapace prolonged posteriorly to form a parallel-sided neck (Fig. 1), and from *holmi* new species by having the median lobe of the tegulum (MLT) large, with bulb length less than  $2 \times$  length MLT, tegulum nearly hidden between MLT and embolus (Figs. 30, 56).

**Description.**—*Male (holotype)*: Total length 2.66. Carapace, palpal coxae, labium and sternum dark red-brown, unmarked; coxae, trochanters, legs and palpi yellow-gray, unmarked except for dark basal annulus on femur IV; abdomen dark gray, venter and sides unmarked, dorsum with yellow-white outlining anteromedian parallel and postero-



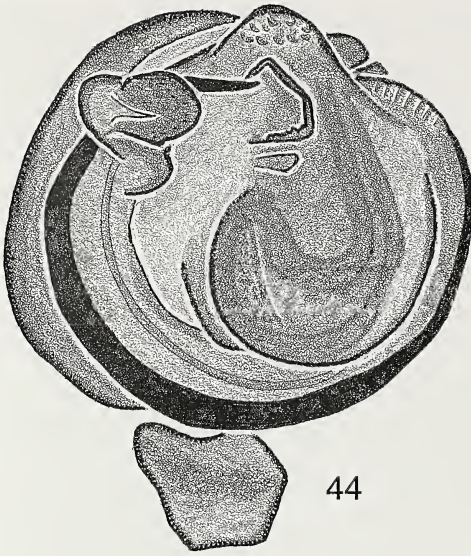


Figures 41–43.—*Scharffia nyasa* new species. 41, Female, dorsal; 42, Female, ventral; 43, Male, lateral.

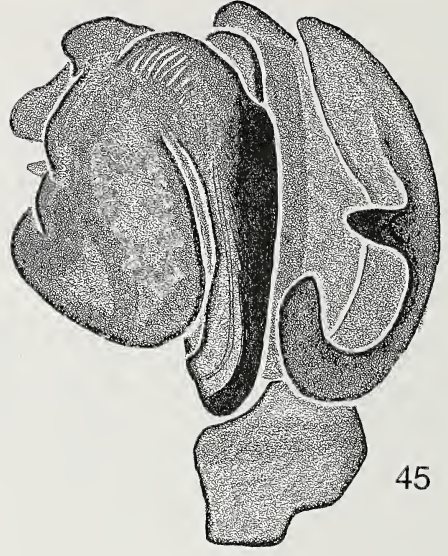
lateral converging longitudinal dark marks (Fig. 1). Carapace 1.26 long, 0.61 wide, 0.37 high, greatly prolonged posteriorly to form narrow neck meeting abdomen; PER 0.40 wide, AER 0.39 wide, OAL 0.18; ratio AM: AL:PM:PL, 1.27:1.0:1.09:1.27, PM diameter 0.06. Clypeus 0.18 high, chelicerae 0.27 long. Sternum 0.68 long, 0.59 wide; labium 0.10 long, 0.16 wide; palpal coxae 0.19 long, 0.16 wide. Leg measurements (femur + patella +

tibia + metatarsus + tarsus = [Total]): I: 2.15 + 0.23 + 1.98 + 1.81 + 0.81 = [6.98]; II: 1.28 + 0.21 + 1.04 + 0.92 + 0.53 = [3.98]; III: 0.85 + 0.19 + 0.59 + 0.53 + 0.45 = [2.61]; IV: 1.21 + 0.19 + 0.91 + 0.76 + 0.42 = [3.49]; Palp: 0.23 + 0.07 + 0.10 + (absent) + 0.25 = [0.65]. Palp (Figs. 30, 31, 54–57) with RMP short, pointed, PC very broad in lateral view; tegulum apex raised, weakly wrinkled, MLT very large and sparsely den-

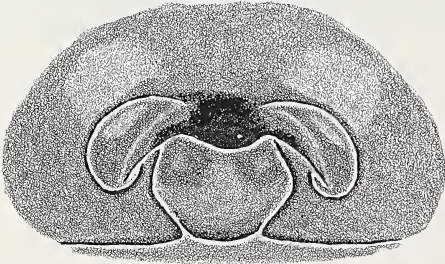




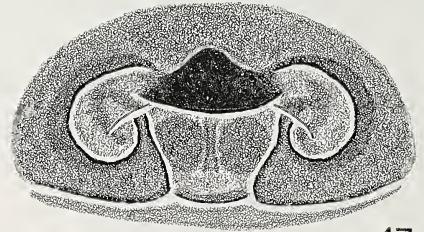
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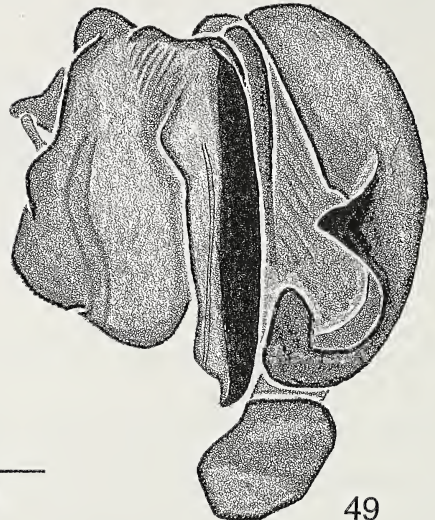
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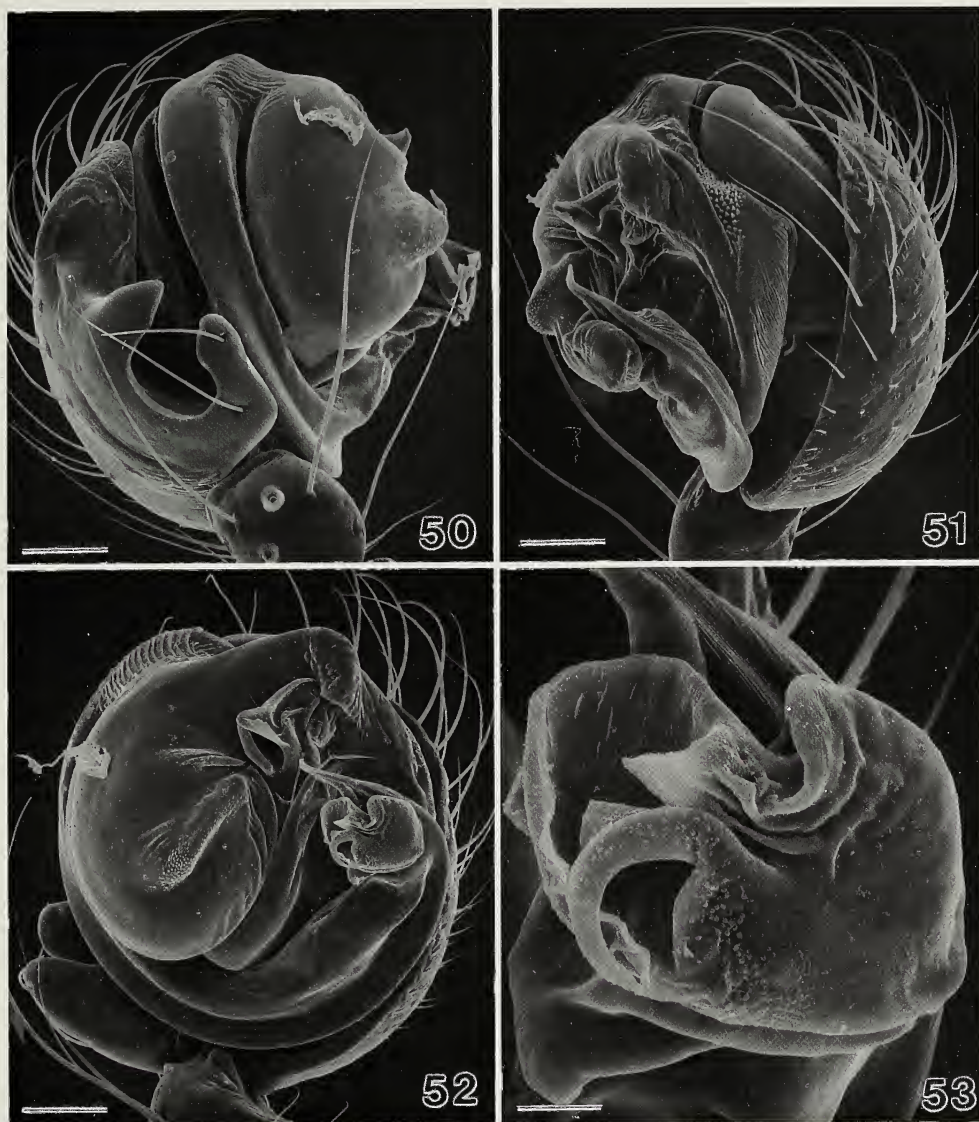


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0.1 mm

Figures 44–49.—*Scharffia*. 44, 45, *Scharffia chinja* new species, holotype, left male palpus; 44, Ventral; 45, Retrolateral; 46, *Scharffia chinja* new species, female, from Uzungwa, epigynum, ventral; 47, *Scharffia nyasa* new species, female, epigynum, ventral; 48, 49, *Scharffia nyasa* new species, left male palpus; 48, Ventral; 49, Retrolateral.





Figures 50–53.—*Scharffia nyasa* new species, right male palpus. 50, Retrolateral; 51, Prolateral; 52, Ventral; 53, Parembolic process. (Scale bars for Figs. 50–52 = 50  $\mu$ m, Fig. 53 = 10  $\mu$ m.)

ticulate over wide median area, tegulum hidden beneath; C simple, narrow; PP absent.

*Female:* Unknown.

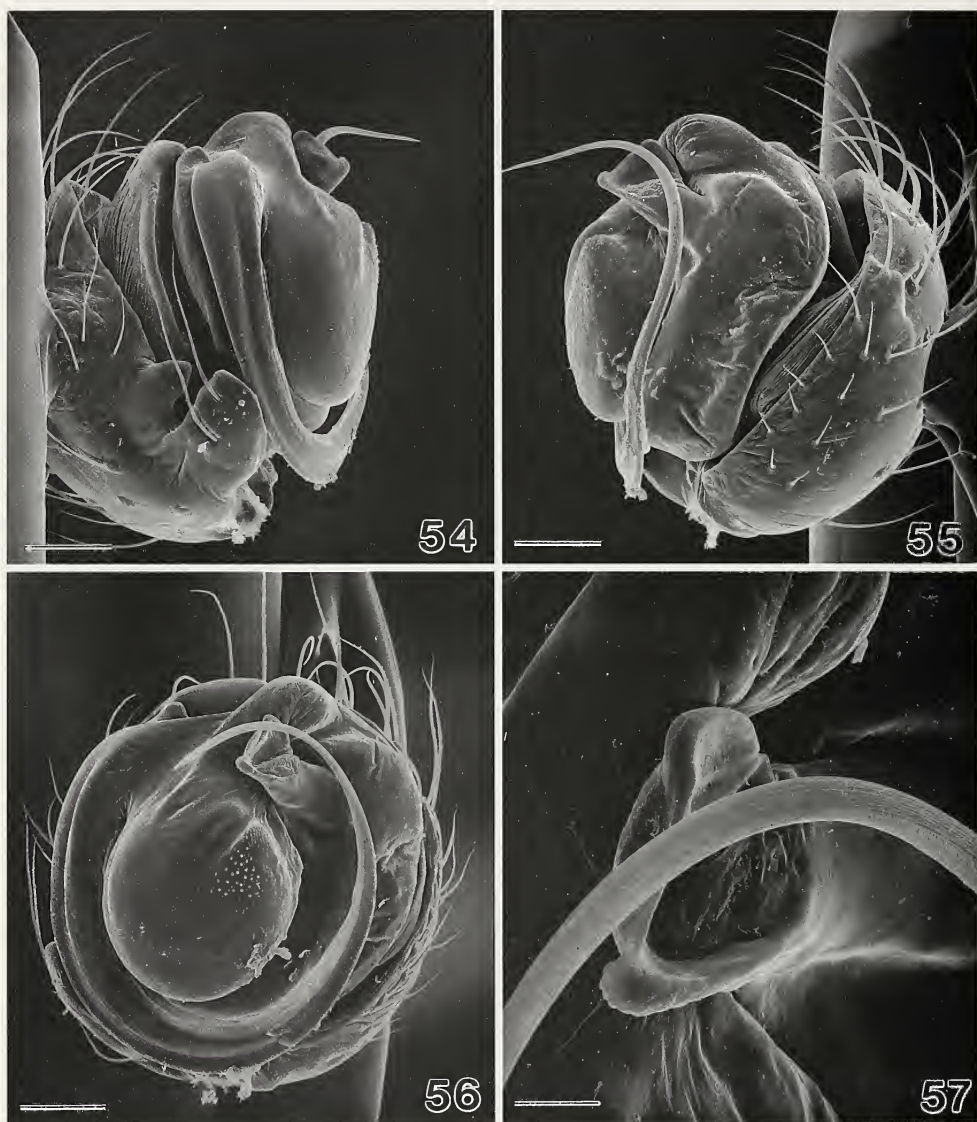
**Natural history.**—The specimen was collected on a hilltop in shade beneath tall umbrella acacias with an understory of grass and stones, either from tree bark or beneath objects on the ground. This dry site was more than 50 km from moist forest (E. Ross, pers. comm.).

**Distribution.**—Known only from the type locality (Fig. 58).

**Material examined.**—Only the type specimen.

## DISCUSSION

Synapomorphies for *Scharffia* are the elongate sternum (length greater than  $1.15\times$  width: Figs. 21, 36) and elongate abdominal petiole. The sternal form is unique within the Cyatholipidae and Synotaxidae. Within these families an annulate anterior abdominal petiole (Figs. 11, 26) is uniquely shared with *Alaranea* Griswold 1997 from Madagascar, and is a synapomorphy uniting these genera:



Figures 54–57.—*Scharffia rossi* new species, holotype, right male palpus. 54, Retrolateral; 55, Prolateral; 56, Ventral; 57, Conductor. (Scale bars for Figs. 54–56 = 50  $\mu\text{m}$ , Fig. 57 = 12.5  $\mu\text{m}$ .)

that of *Scharffia* is longer than that of *Alaranea*, which in turn has a unique dorsal horn (Griswold 1997, figs. 4, 68, 94). Synapomorphies within *Scharffia* are the carapace prolonged posteriorly into a neck uniting *holmi* new species (Fig. 32) and *rossi* new species (Fig. 1) and an abdominal petiole longer than 0.24 carapace (Figs. 11, 18) uniting these species with *chinja* new species.

Are *Scharffia* components of the Afromontane biota (White 1978; Griswold 1991)? Whereas they occur in montane forests of the Eastern Arc mountains and Albertine Rift,

they are also recorded from lowland forests and savanna woodland (Fig. 58). Unlike the montane east African Linyphiidae studied by Scharff (1992, 1993), which typically had endemic species on each mountain within the Eastern Arc, *Scharffia chinja* new species is widespread. Whether *Scharffia* are very old (perhaps older than the mountains) and slow to differentiate, or readily dispersed, cannot be easily resolved. Occurrence of *Scharffia* in lowland forest (*chinja*) and open, dry country (*rossi*) suggests that for *Scharffia*, the Eastern Arc mountains may not be effectively isolated



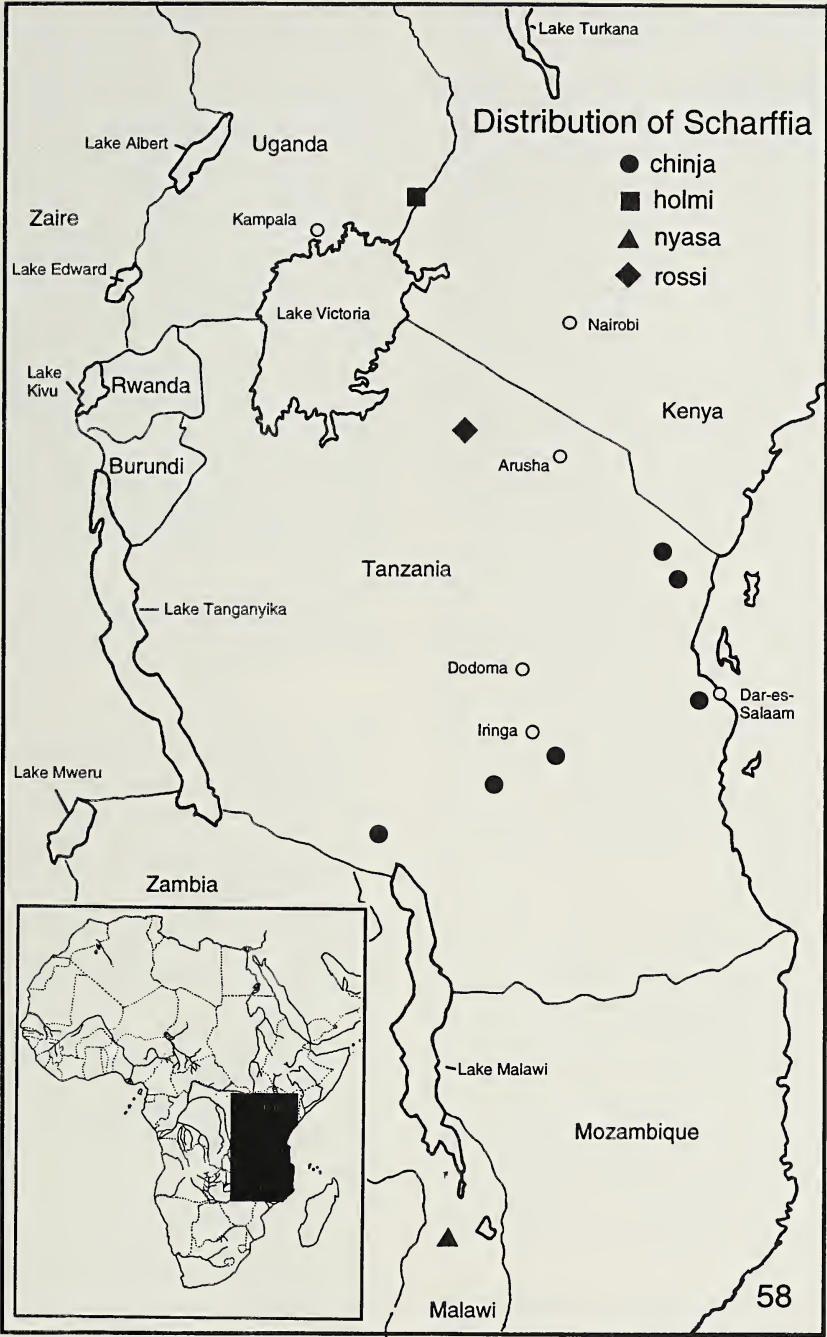


Figure 58.—Distribution of *Scharffia*.

from one another. On the other hand, the distribution of the sister group of *Scharffia* (*Alaranea*, in Madagascar) is consistent with the Afromontane biogeographic pattern detailed for spiders (Griswold 1991) in which Madagascar and the montane forests of eastern Af-

rica are sister areas. Several groups of spiders, including *Phyxelida* and the *Lamaika* group of the Amaurobiidae Phyxelidinae (Griswold 1990), and *Ulwembua* and *Alaranea* plus *Scharffia* of the Cyatholipidae (Griswold 1997), show this intercontinental disjunction,

suggesting that their distribution is not the result of accidental dispersal. Their distribution may date from times of former connection or at least greater proximity between Madagascar and eastern Africa, perhaps in the Mesozoic (Rabinowitz et al. 1983). Given the possible great age of this sister-group disjunction, *Scharffia* appears to be another component of an ancient Afromontane biota.

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The manuscript was read and criticized by Norman Platnick and D. Ubick.

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## GROWTH RATES IN THE SCORPION *PSEUDOUROCTONUS REDDELLI* (SCORPIONIDA, VAEJOVIDAE)

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**ABSTRACT.** Members of the family Vaejovidae are the dominant species of scorpion in much of western North America, yet relatively little is known of the life histories in this group. In this paper I present data on growth rates of a single litter of *Pseudouroctonus reddelli*, a troglophilic vaejovid from central Texas. From an initial litter of 53 juveniles, one individual reached instar 8. Nearly 75% of this litter died during instar 2 or 3; this mortality rate was quite high, but consistent with other laboratory studies on vaejovid growth. A comparison with adults from this population suggested that *P. reddelli* mature at instar 9 for both males and females. Progression factors for two morphological measures during the early instars were more often below the predicted theoretical value of 1.26, while the progression factor for mass was close to the theoretical value of 2.0. No sexual dimorphism in growth rates was observed for instars 2–4. In comparison with other vaejovids, *P. reddelli* has a larger litter size, shorter instar 1 duration but comparable durations for instars 2–4, and lower morphological progression factors.

The scorpion family Vaejovidae Thorell 1876 is a relatively large group, consisting of at least 150 species (Sissom 1990; Stockwell 1992). Recently, Stockwell (1992) revised the Vaejovidae to include only the nominate subfamily (Vaejovinae Thorell 1876), which includes species distributed from southern Canada through the United States into central Mexico. Although this family contains probably the most studied species of scorpion [*Smeringerus mesaensis* (Stahnke 1957); see Polis 1993 and references therein], relatively little is known of the ecology or life history for the majority of vaejovids. For example, Polis & Sissom (1990) give life history data, such as litter size or number of molts to maturity, for only 18 species.

One of the more interesting vaejovids, both ecologically and taxonomically, is *Pseudouroctonus reddelli* (Gertsch & Soleglad 1972), a relatively large, dark-colored species distributed throughout much of central Texas (Gertsch & Soleglad 1972; Stockwell 1986). As with other vaejovids, individuals may be found under surface debris such as rocks or logs. However, *P. reddelli* is unusual in that it is troglophilic, with the majority of specimens having been captured from caves (Gertsch & Soleglad 1972; Stockwell 1986)

despite the lack of any obvious adaptations for cave dwelling (such as lack of eyes or pigmentation, or elongated appendages) as seen in troglobitic scorpions. Individuals are usually located fairly close to the cave entrance (within the initial 50–100 m).

The taxonomic status of *P. reddelli* remains unsettled. It was initially described by Gertsch & Soleglad (1972) as *Vaejovis reddelli* before being transferred to a new genus, *Pseudouroctonus* Stahnke 1974. Subsequent authors (Stockwell 1986; Sissom 1990), noting that characters used to separate *Pseudouroctonus* from *Vaejovis* were not unique to either group, returned *reddelli* to *Vaejovis*. In the most current treatment, Stockwell (1992) has transferred this species, along with species in the *minimus* group of *Vaejovis*, back to *Pseudouroctonus*. I have chosen to utilize this most recent nomenclature while acknowledging that there is still debate both to the validity of *Pseudouroctonus* and the placement of *reddelli* within a genus.

In this paper I analyze growth rates (for both mass and morphometric measures) from a single litter of laboratory-reared *P. reddelli*. These data represent the first life history information for this species, as well as the first data on changes in mass through ontogeny in a laboratory-reared scorpion.



## METHODS

**Study site.**—The female whose litter was used for this study was collected from Kickapoo Caverns State Park, located on the border of Kinney and Edwards Counties approximately 37 km north of Brackettville, Texas. The park lies on the southwestern Edwards Plateau, a region of limestone hills surrounding extensive canyons, dominated by Ashe juniper (*Juniperus ashei*) and plateau live oak (*Quercus fusiformis*) (Lockwood et al. 1993). Underlying the plateau are several underground aquifers which have flowed along major fault lines to create a series of caves and artesian wells (Veni 1988). Within the park, a small population of *P. reddelli* exists in Kickapoo Caverns, a series of chambers near the eastern park boundary. From 1992–1994 a total of seven *P. reddelli* was captured from this cave (6♂, 1♀). No *P. reddelli* have been observed on the surface at the park, where the dominant scorpion species is *Centruroides vittatus* (Say 1821).

**Rearing of juveniles.**—On 20 July 1993 a single gravid female *P. reddelli* was collected from inside Kickapoo Caverns. This female was found after sunset, approximately 40 m from the cavern entrance along a rock outcropping, by using a portable flashlight with an ultraviolet bulb. Upon return to the laboratory the female was weighed (to the nearest gram), then housed in an 18.5 × 7.5 × 9 cm plastic container with a sand substrate (~ 0.5 cm deep). A wet paper towel was provided to serve as a source of moisture and cover object. The laboratory was maintained on a 14:10 h light:dark photoperiod at a mean temperature of 27.1 °C (range 24–28 °C). The female was fed one adult cricket (*Acheta domestica*) upon return to the laboratory and was offered one adult cricket every three weeks thereafter until giving birth; she was not fed while carrying offspring.

The female gave birth nearly three months after capture, on 10 October 1993. The newborn scorpions (scorplings) oriented themselves in rows on the female's back, as is commonly seen in many species of the genus *Vaejovis* (e.g., Williams 1969). The juveniles molted into instar 2 after 6 days, and dispersed from the female 6–7 days following molting. Immediately after dispersal, each juvenile was individually weighed to the nearest 0.1 mg,

then housed in a 9 cm diameter petri dish containing a small square of paper towel. The petri dishes were stacked and kept in a larger (27.5 × 40 × 16 cm) plastic container with paper towels on the bottom which were moistened daily. This allowed for the maintenance of adequate humidity without having to wet directly the paper towel in each petri dish (excessive watering can drown immature scorpions and hasten growth of mold on uneaten food). Every third day, the top petri dish in a stack was rotated to the bottom to minimize the effect of any moisture gradient within the box. Every third feeding day I transferred each juvenile to a clean petri dish. Following the molt into instar 4 I added a layer of sand 1–2 mm deep to the petri dish. Rearing occurred under the same conditions of temperature and photoperiod as described above.

Juveniles were maintained on hatchling crickets (one week old or less; mean feeding interval = 6.05 days, range 3–10 days), with the number and/or size of the crickets varying with the scorpion's instar. In general, I doubled either the number of crickets or the size of the cricket offered with each increase in instar. Following the molt into instar 6, each juvenile was moved into a container similar to that which housed the female and fed one adult cricket every three weeks.

With the exception of the molt from instar 2 to instar 3 (due to mechanical difficulties with the balance used), juveniles were weighed to the nearest 0.1 mg following each molt. From the exuvium at each molt (or following the death of an individual) I measured three morphological characters [carapace length, metasomal segment V length, and body (prosomal + mesosomal) length] to the nearest 0.01 mm using an American Optical® dissecting microscope equipped with an optical micrometer calibrated at 10×. Body length was computed as the sum of carapace length plus mesosoma length; individual mesosomal segments were not measured separately, as has been recommended by some authors (Stahnke 1970; Sissom et al. 1990). Where possible, I determined sex by looking for the presence of genital papillae, a male secondary sexual characteristic (these were first observed in juveniles during instar 4).

For carapace length, metasomal segment V length, and mass I calculated a progression factor (P.F.) by dividing the value at one instar



by the corresponding value at the preceding instar (e.g., carapace length at instar 4 divided by carapace length at instar 3). Progression factors were then compared to theoretical values (for mass,  $PF = 2.0$ ; for length,  $PF = 1.26$ , the cube root of 2.0) commonly used to predict the number of molts to maturity in scorpions (reviewed in Francke & Sissom 1984). Finally, I calculated the instar duration as the number of days between successive molts. All statistical analyses were done using the STATISTICA for Windows (vers. 4.5) computer package (StatSoft 1993).

## RESULTS AND DISCUSSION

The gravid female had an initial mass of 1250 mg when returned to the laboratory and a mass of 778 mg following offspring dispersal. A total of 53 offspring dispersed from the female; no evidence of cannibalism of juveniles was observed either during birth or while the female carried the offspring. This litter size was relatively high for a vaejovid and is over twice the family average of 23 (Polis & Sissom 1990). Only *V. spinigerus* (Wood 1863), with 66, has a higher reported value (Stahnke 1966). The mean offspring mass following dispersal was 5.8 mg, giving a total litter mass (TLM) of 307 mg. As a measure of reproductive investment by the female I calculated relative clutch mass (RCM) as TLM divided by post-dispersal female mass; this produced a value of 0.395. This represents a lower bound on female investment, as juveniles lose mass while being carried by the female (Formanowicz & Shaffer 1993). This value was below the mean RCMs reported for *Centruroides vittatus* (0.47–0.53, Formanowicz & Shaffer 1993; Brown & Formanowicz 1995), and for *Diplocentrus* sp. and *V. waueri* Gertsch & Soleglad 1972 (0.49 and 0.55, respectively; Brown & Formanowicz 1996).

One individual died following dispersal but prior to the first weighing, leaving 52 juveniles in the initial sample. Of these, 22 molted into instar 3 (42.3% success rate), 14 molted into instar 4 (26.9% success rate), 10 molted into instar 5 (19.2% success rate), four molted into instar 6 (7.7% success rate), two molted into instar 7 (3.8% success rate), and one molted into instar 8. These success rates are low, but comparable to other studies of vaejovid post-birth development (e.g., Francke

1976; Sissom & Francke 1983; Francke & Sissom 1984). Death was usually associated with molting. Occasionally this was due to unknown causes, but more often the molting process had begun while a cricket was in the container, and the juvenile had been preyed upon while helpless during emergence from the old exoskeleton.

The data for the growth rates from this litter of *P. reddelli* are summarized in Table 1. The duration of instar 1 (6 days) is shorter than previously reported for any vaejovid, and is less than half the family mean of 12.6 days (Polis & Sissom 1990). The average duration of instars 2–4 is quite consistent at around 100 days, although substantial variability within an instar does exist, more so in instars 2 and 4 than in instar 3. The duration increases during instars 5 and 6 before decreasing again during instar 7; these values should be regarded with some caution because of lower sample sizes. For the two comparisons for which I had a reasonable ( $\geq 10$ ) sample size, the duration of time spent in one instar had no effect on the duration of the succeeding instar (Pearson's product-moment correlation: instar 2 vs. instar 3:  $r = -0.41$ ,  $P = 0.09$ ,  $n = 18$ ; instar 3 vs. instar 4:  $r = 0.29$ ,  $P = 0.41$ ,  $n = 10$ ). The durations of instars 2–5 are similar to those reported for *Vaejovis bilineatus* Pocock 1898 (Sissom & Francke 1983) and *Uroctonus mordax* Thorell 1876 (Francke 1976), but considerably shorter than those for *V. coahuilae* Williams 1968 (Francke & Sissom 1984). It should be noted that differences in rearing and feeding regimes existed between my study and these others, primarily in photoperiod and prey; these may strongly affect the growth rates observed (see below and Polis & Sissom 1990).

A bivariate morphometric plot of carapace length versus metasomal segment V length (Fig. 1) showed an overall slight positive allometric relationship. In general, the carapace is longer than metasomal segment V for instars 2–4 and shorter than metasomal segment V for instars 5–8; this pattern appears to be common in vaejovids (Francke 1976; Sissom and Francke 1983; Francke & Sissom 1984). Within an instar, these two characters were not correlated for instar 2 ( $r^2 = 0.01$ ,  $P = 0.47$ ,  $n = 47$ ), but were significantly positively correlated for instar 3 ( $r^2 = 0.56$ ,  $P < 0.001$ ,  $n = 20$ ), instar 4 ( $r^2 = 0.80$ ,  $P < 0.001$ ,  $n =$



Table 1.—Growth rates for a single litter of 52 *Pseudouroctonus reddelli*. Data are given as mean  $\pm$  SD above, with ranges (sample size *n*) below. Where there are less than three data points, only the range is given.

Instar	Mass (mg)	Body length (mm)	Carapace length (mm)	Metasomal segment V length (mm)	Duration (days)
2	5.79 $\pm$ 0.51 4.3–7.2 (53)	3.98 $\pm$ 0.75 3.36–6.35 (44)	1.49 $\pm$ 0.05 1.38–1.57 (47)	1.39 $\pm$ 0.04 1.29–1.48 (50)	99.6 $\pm$ 14.1 74–135 (35)
3		4.28 $\pm$ 0.64 3.85–5.95 (17)	1.72 $\pm$ 0.07 1.61–1.84 (20)	1.64 $\pm$ 0.08 1.48–1.80 (21)	103.1 $\pm$ 10.4 87–117 (18)
4	22.5 $\pm$ 3.7 17–31 (12)	5.38 $\pm$ 1.15 4.20–7.64 (14)	1.98 $\pm$ 0.17 1.71–2.26 (14)	1.97 $\pm$ 0.13 1.80–2.21 (14)	97.7 $\pm$ 17.2 69–125 (10)
5	44.8 $\pm$ 11.6 29–69 (10)	8.12 $\pm$ 1.71 5.63–10.28 (9)	2.60 $\pm$ 0.20 2.26–2.93 (9)	2.63 $\pm$ 0.23 2.31–3.04 (10)	154.5 $\pm$ 35.2 107–187 (4)
6	94.2 $\pm$ 16.0 73–111.4 (4)	9.77 $\pm$ 1.83 8.13–12.15 (4)	3.13 $\pm$ 0.24 2.90–3.40 (4)	3.30 $\pm$ 0.24 3.04–3.62 (4)	151–192 (2)
7	201–224 (2)	11.7–15.1 (2)	3.82–4.11 (2)	4.01–4.39 (2)	109 (1)
8	434.4 (1)	18.3 (1)	5.16 (1)	6.08 (1)	

14) and instar 5 ( $r^2 = 0.91$ ,  $P < 0.001$ ,  $n = 9$ ). Carapace length was significantly positively correlated with mass (cube-root transformed to equalize dimensionality with length) within instars 2, 4, and 5 (Figs. 2–4). This relationship is relatively weak initially ( $r^2 = 0.12$  for instar 2,  $n = 47$ ), but becomes quite strong during later instars [ $r^2 = 0.85$  and  $0.96$ , respectively, for instar 4 ( $n = 12$ ) and instar 5 ( $n = 9$ )]. To examine whether there were differences among sexes in growth rates, I performed a series of *t*-tests using the 15 individuals (9♂, 6♀) for which I was able to identify sex positively. For instars 2–4, the results (Table 2) showed no dimorphism between the sexes in mass, instar duration or morphometric measures, with the exception of metasomal segment V length in instar 4 (females longer than males). Dimorphism among adults in this population may exist, as all of the adult males captured have been larger than the adult female; however, the sample size of adults is far too small to make any definitive statements, and other authors (Gertsch & Sologlad 1972) have described females larger than males.

The mean progression factors (P.F.'s) for carapace length and metasomal segment V length (Table 3) were in general below the theoretical value of 1.26, especially during early development. This was more pronounced for carapace length than for meta-

somal segment V length. These morphological P.F.'s are less than those previously reported for the Vaejovidae. For carapace length and metasomal segment V length, respectively, average P.F.'s were 1.24 and 1.29 for *V. coahuilae* (Francke & Sissom 1984), 1.26 and 1.32 for *V. bilineatus* (Sissom & Francke 1983), and 1.31 and 1.41 for *U. mordax* (Francke 1976). As with these three species, the carapace grows less rapidly (P.F.'s were lower) than does the last metasomal segment in all instars of *P. reddelli*. The mean P.F. for mass (Table 3) was above the theoretical value of 2.0 in three of the four ratios, although sample size was low in all groups. Mass progression factors have not been reported previously for any vaejovid.

The one juvenile to reach instar 8 was a male, as determined by the presence of genital papillae. A comparison of the morphological measurements from this individual (Table 1) to measurements of field-caught *P. reddelli* males suggests that this may be an immature, and thus males may reach sexual maturity at instar 9. Three adult males captured from Kickapoo Caverns in March 1993 had an average carapace length of 6.45 mm and an average metasomal segment V length of 8.22 mm. Both of these measurements are considerably larger than those for the instar 8 individual (Table 1), and would represent progression factors from instar 8 to instar 9 of

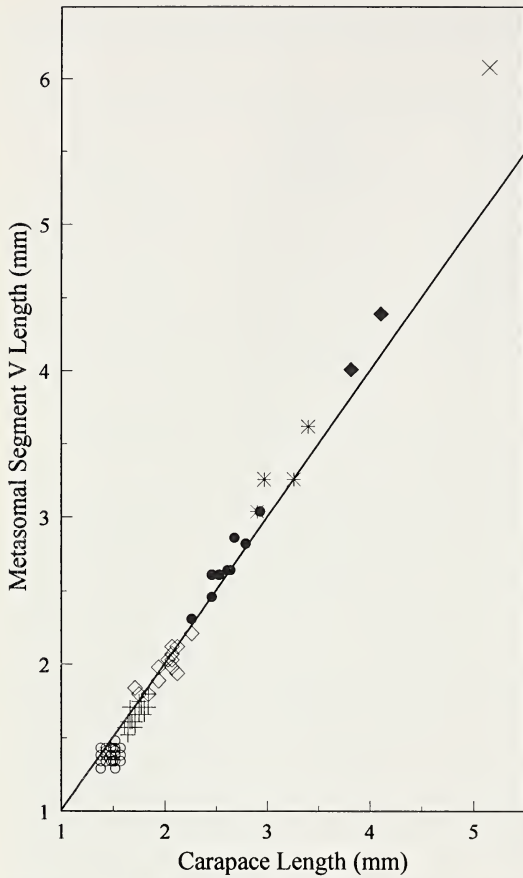
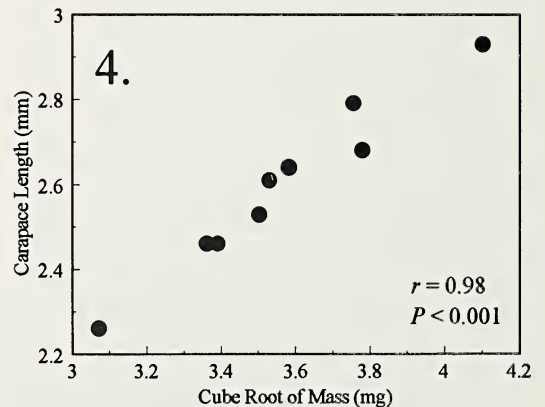
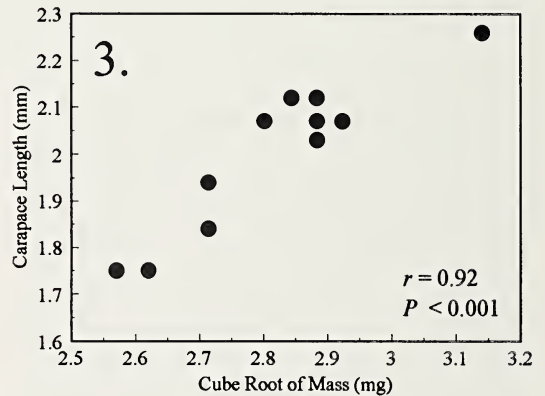
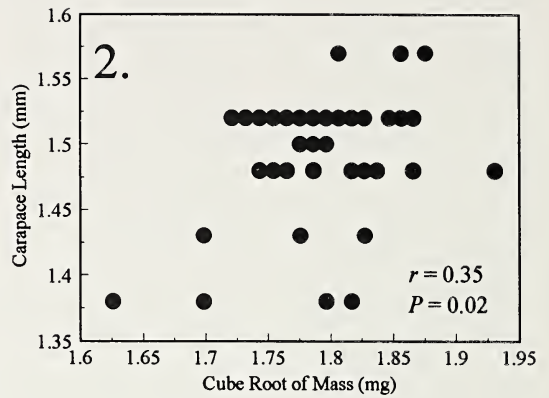


Figure 1.—Bivariate plot of carapace length (in mm) versus metasomal segment V length (in mm) for a single litter of *Pseudouroctonus reddelli*. Symbols are as follows: open circles (○) = instar 2; plus signs (+) = instar 3; open diamonds (◇) = instar 4; closed circles (●) = instar 5; asterisks (\*) = instar 6; closed diamonds (◆) = instar 7; crosses (×) = instar 8. The line indicates a 1:1 relationship between the two measures.

1.25 for carapace length and 1.35 for metasomal segment V length. These P.F.'s are within the range of values calculated from earlier instar growth data. Among females from this litter, the two oldest individuals died during instar 5. Using the average P.F.'s from instar 6–8 males (1.22 for carapace length, 1.26 for metasomal segment V length), these females would be expected to reach the adult female's size (carapace length = 6.36 mm, metasomal segment V length = 7.35 mm) at instar 9.

Thus, from the laboratory data it appears that maturity in *P. reddelli* is reached at instar 9 for both sexes. Only two species have pre-



Figures 2–4.—Plots of the cube root of mass (in  $\text{mg}^{1/3}$ ) versus carapace length (in mm) in *Pseudouroctonus reddelli*.  $r$  represents the Pearson product-moment correlation between the two variables. 2, Instar 2; 3, Instar 4; 4, Instar 5.



Table 2.—Variation between sexes during instars 2–4 in a subset of 15 individual juveniles (9 males, 6 females) from a litter of *Pseudouroctonus reddelli*. Means are reported for each variable. Within each instar, comparisons were made using a *t* test. ns = not significant. \* = significant at *P* = 0.05.

Instar	Sex	Mass (mg)	Carapace length (mm)	Metasomal segment V length (mm)	Duration (days)
2	male	5.95	1.47	1.4	95
	female	5.6	1.5	1.39	97.3
	<i>t</i>	1.31 ns	0.97 ns	0.51 ns	0.28 ns
3	male		1.7	1.64	103.7
	female		1.73	1.67	99.8
	<i>t</i>		0.64 ns	0.88 ns	0.69 ns
4	male	21.4	1.92	1.9	92.4
	female	22	1.99	2.02	98
	<i>t</i>	0.34 ns	0.73 ns	1.88*	0.45 ns

viously been found to require as many instars to reach maturity, both members of the family Diplocentridae Peters 1861: *Didymocentrus trinitarius* (Franganillo 1930) (9–10 instars; Armas 1982) and *Diplocentrus whitei* (Gervais 1844) (8–9 instars; Francke 1982). For the Vaejovidae the mean instar at maturity is 6.8, with a range of 6–8 (Polis & Sissom 1990). At this point I have no evidence to suggest that maturity is reached at different instars, either within a sex or between sexes; this phenomenon has been reported for the vaejovid *V. coahuilae* (Francke & Sissom 1984) as well as a number of species from other families (see Polis & Sissom 1990).

Finally, these results should be viewed with caution, for several reasons. First, as has been

noted by other authors (reviewed in Polis & Sissom 1990), both environmental factors (e.g., temperature) and feeding history can have an influence on traits such as gestation time and growth rates, such that laboratory studies and field studies of scorpion life histories may produce conflicting conclusions for a given species. In this study, this may be the case especially for the estimation of the number of molts to maturity, particularly if progression factors are sensitive to environmental variation (as seems likely). Second, the data presented here represent results from a single litter, so that any genetic variation in reproductive investment patterns (e.g., among individuals or populations) was not uncovered. Third, when comparing these results to those

Table 3.—Progression factors (PF) for carapace length, metasomal segment V length, and mass in *Pseudouroctonus reddelli*. Data are given as mean ± SD above, range (sample size *n*) below. Where there are less than three data points, only ranges are given.

PF	Carapace length	Metasomal segment V length	Mass
2 → 3	1.17 ± 0.05	1.19 ± 0.05	
	1.09–1.29 (20)	1.10–1.28 (21)	
3 → 4	1.15 ± 0.07	1.18 ± 0.06	
	1.00–1.23 (14)	1.11–1.29 (14)	
4 → 5	1.29 ± 0.03	1.35 ± 0.05	2.03 ± 0.21
	1.26–1.34 (9)	1.28–1.45 (10)	1.71–2.35 (9)
5 → 6	1.22 ± 0.07	1.27 ± 0.04	2.23 ± 0.21
	1.13–1.28 (4)	1.23–1.32 (4)	2.04–2.52 (4)
6 → 7	1.17–1.21 (2)	1.21–1.23 (2)	2.01–2.04 (2)
7 → 8	1.26 (1)	1.38 (1)	1.94 (1)

from other studies on scorpion growth, it is important to take strongly into account differences in rearing and feeding conditions, whether the study was field- or lab-based, and whether individuals from various populations were used, since all of these factors are potential influences on variation in scorpion growth and reproduction.

#### ACKNOWLEDGMENTS

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## A COMPARISON OF CAPTURE THREAD AND ARCHITECTURAL FEATURES OF DEINOPOID AND ARANEOID ORB-WEBS

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**ABSTRACT.** Orb-webs constructed by the superfamilies Deinopoidea and Araneoidea share a common architecture, but differ in both their orientation and the type of capture thread that they contain. This study uses transformational analyses to determine which web features these clades share and which features are unique to the Araneoidea and may be associated with changes in web orientation and capture thread composition. It examines relationships among spider weight, the cross sectional area of capture thread axial fibers, and features of orb-web architecture in four species of the Family Uloboridae that construct horizontal orb-webs containing cribellar thread and four araneoid species that construct vertical webs containing adhesive capture thread. In both groups, spider weight was positively related to web area and the number of radii in a web were positively related to the number of spirals. In uloborids, weight was negatively related to the number of spirals per web area and axial fiber cross sectional area was positively related to the number of radii per capture spiral turn. In araneoids, spider weight was positively related to axial fiber cross sectional area. The number of radii per capture spiral turn was greater in uloborid webs, and the weight-specific axial fiber cross sectional area was greater in araneoid webs. Many of the features that distinguish araneoid orb-webs appear to equip them to absorb the greater forces of prey strike that are associated with a vertical orb-web orientation.

Orb-weaving spiders that produce cribellar capture threads and belong to the superfamily Deinopoidea and those that produce adhesive capture threads and belong to the superfamily Araneoidea share a common web architecture by virtue of their common ancestry (Coddington 1986a,b, 1990a,b; Coddington & Levi 1991). The transition from dry, cribellate orb-webs to viscous, adhesive orb-webs is associated with an increase in species diversity (Bond & Opell pers. obs.) and with changes in web orientation and capture thread composition that have the potential to alter orb-web architecture and performance. This study uses phylogenetic techniques to determine which web features are shared by both deinopoid and araneoid orb-weavers and which features are unique to each clade and may thus reflect differences in the operational dynamics of their webs. It examines associations among spider weight, the cross sectional area of capture thread axial fibers, and orb-web architectural features. These relationships provide a better understanding of factors that have constrained the design and dynamics of spider orb-webs and changes that have been associ-

ated with the evolution of araneoid orb-weavers.

Deinopoid and araneoid orb-weaving spiders are distinguished by differences in web orientation and in the material that covers the axial fibers of their prey capture threads. The horizontal orientation of orb-webs spun by members of the Deinopoidea is plesiomorphic for the Orbiculariae, whereas the vertical orientation of orb-webs constructed by the Araneoidea is a synapomorphy of this clade (Bond & Opell pers. obs.). As a result of their vertical orientation, araneoid orb-webs tend to intercept faster flying insects and, therefore, are often required to absorb greater forces of impact than are cribellate orb-webs (Craig 1987a; Eberhard 1989). Thousands of fine cribellar fibrils surround the axial fibers of cribellar capture threads produced by the Deinopoidea (Eberhard 1988; Eberhard & Pereira 1993; Opell 1990, 1993, 1994a-c, 1995, 1996; Peters 1983, 1984, 1986, 1992), whereas a chemically complex viscous solution that coalesces into droplets surrounds the homologous axial fibers of adhesive capture threads produced by orb-weaving Araneoidea (Peters

1995; Tillinghast et al. 1993; Townley et al. 1991; Vollrath 1992; Vollrath et al. 1990; Vollrath & Tillinghast 1991). Each of the droplets of adhesive thread draws in a length of axial fiber that can be played out when tension on the thread increases (Vollrath & Edmonds 1989). This windlass increases the extensibility of adhesive threads (Köhler & Vollrath 1995) and, thereby, helps maintain web tension and probably reduces capture thread tangling under windy conditions.

Differences in architecture can affect orb-web performance. For example, among araneoid spiders, orb-webs that have a large number of radii relative to the number of spiral turns they contain (radius-rich webs) more effectively stop heavier or faster flying prey than do radius-poor webs (Craig 1987b; Eberhard 1986). Some of these differences are associated with differences in spider weight. In araneoid orb-weavers, spider weight is directly related to the diameter of the axial fibers within a capture thread (Craig 1987a) and in uloborid orb-weavers, spider weight is directly related to web area and web stickiness (Opell 1996).

Web features such as these have been examined principally among the Araneoidea (e.g., Craig 1987a,b; Eberhard 1986; Risch 1977; Witt et al. 1968) using correlation or regression techniques. Since these studies were done, transformational analysis has become the accepted method of analyzing relationships of features in a phylogenetic context (Harvey & Pagel 1991). Therefore, I use this comparative method to examine relationships among spider weight, the cross sectional areas of capture thread axial fibers, and features of web architecture. This analysis found five significant relationships. Two relationships are shared by both deinopoid and araneoid clades and are hypothesized to be synapomorphies of the Orbiculariae. Two relationships are unique to the Deinopoidea and one relationship is unique to the Araneoidea. Changes in these three relationships are hypothesized to be associated with the origin of araneoid orb-weavers.

## METHODS

**Species studied.**—Ten species of web-spinning spiders were studied. Their phylogenetic relationship is shown in Fig. 1. Data for the five araneoid species are taken from the stud-

ies of Craig (1987a,b). To these I added data for five species of the family Uloboridae. These species were selected to represent the family's diversity by including representatives of its major clades (Coddington 1990b) and included the orb-weavers, *Waitkera waitakerensis*, *Siratoba referena*, *Uloborus glomus*, and *Octonoba sinensis* and the triangle-web species *Hyptiotes cavatus*. *Hyptiotes cavatus* was not included in the final comparison of web features, but was used to add resolution to the phylogenetic analysis that generated data used in this comparison. Voucher specimens of each species are deposited in Harvard University's Museum of Comparative Zoology.

**Web measurements.**—Orb-web architecture is sometimes portrayed as being highly stereotypic and species-specific. For example, Foelix (p. 128, 1996) states that "The number of radii varies little within a particular species of orb weaver, and is often characteristic of that species. . . . These numbers of radii imply that many orb weavers show a species-specific geometry in their webs. It is thus often possible to identify a certain spider solely by its characteristic web structure." However, while acknowledging that "in a local fauna species of orbweavers can often be determined from their webs", Eberhard (p. 342, 1990) documents a number of factors that contribute to intraspecific differences in orb-web architecture and cautions that: "The impression of species-specificity may usually, however, be the product of lack of information. . . . Given the long-standing and repeated documentation of substantial intraspecific variation in at least gross web characteristics such as numbers of radii, spiral loops, spacing between loops, angle of web plane with the vertical, web area, top-bottom asymmetry, and stabilimenta, Levi's prediction that species-specificity will be uncommon seems likely to be correct."

This study attempts to minimize the potential problem of intraspecific variation in uloborid web features by using species means in transformational analyses. As only one web per individual was measured, it does not address the intra-individual variability in web features that may result from differences in nutritional levels or reproductive status. However, the minimum sum of squares algorithm used by the transformational analysis minimizes the hypothesized evolutionary changes



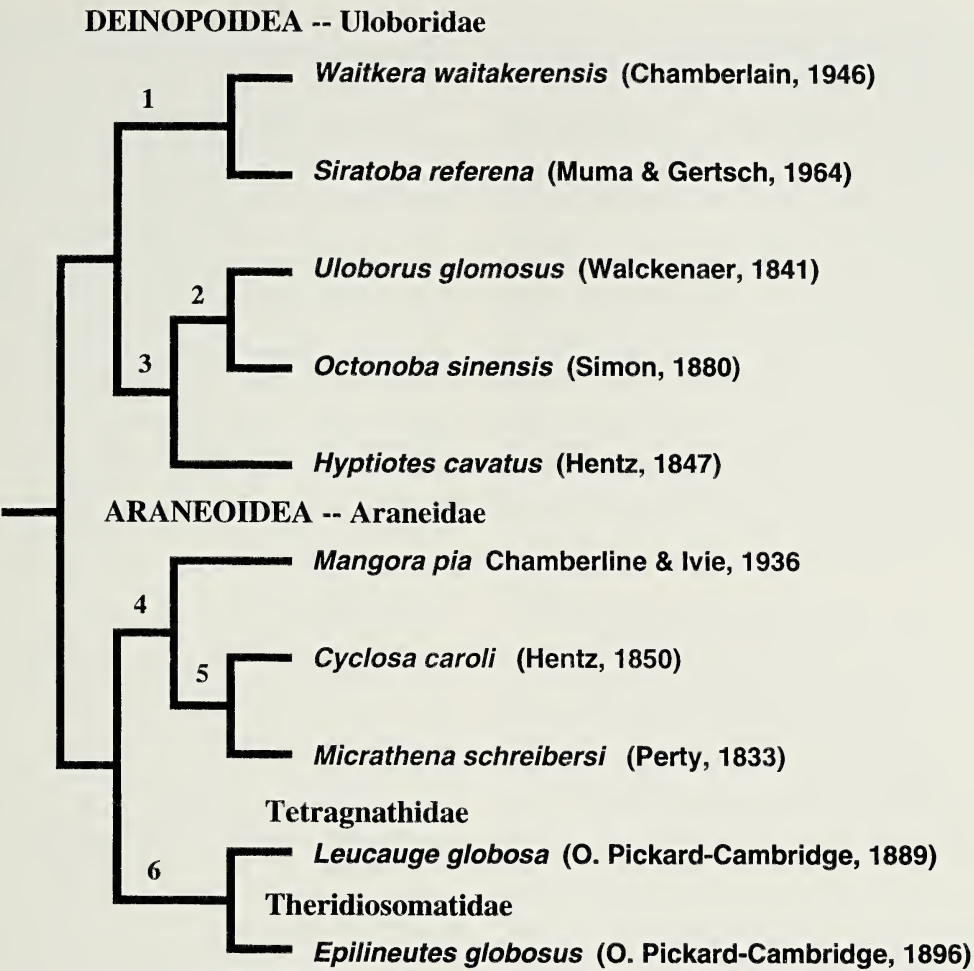


Figure 1.—Cladogram of the species included in this study (from Coddington 1990b; Coddington & Levi 1991; Levi 1985).

that are used in statistical analyses and, thereby, makes the results of these analyses conservative.

I dusted the webs produced by adult females with corn starch to make their threads more visible (Carico 1977) and photographed only webs that were not damaged. I photographed the webs of *W. waitakerensis* in the field and those of *O. sinensis* in a greenhouse. In field photographs of the other three species, it was difficult to distinguish the threads from background vegetation. Therefore, I allowed these spiders to build their webs in individual plastic boxes that contained a framework of wooden dowel rods and photographed these webs against a black background. Spiders were placed into boxes immediately after being collected and were not fed. Those that did

not build a web within three days of capture were released. Boxes were housed in an environmental chamber with a 1 h dawn, 11 h light, and 1 h dusk light cycle. Temperature was maintained at 24 °C and relative humidity ranged from 80% during the night to 70% at dusk and dawn, to 60% during the day.

After photographing a spider's web, I collected and weighed to the nearest 0.00 mg the spider that produced it. Conspecific web capture has not been studied in the species that were included in this study. Therefore, there is a small possibility that some spiders whose webs were photographed may not have actually constructed the webs in which they were found.

It is possible that the boxes in which spiders constructed their webs may have affected the

size of these webs. To assess this for the two orb-weaving species, I determined the mean framework diameter and the maximum capture spiral diameter for each species and compared this with the dimensions of the plastic boxes in which these spiders constructed their webs. Mean framework diameter was computed from the minimum and maximum lengths of straight lines that extended across a web's center to its outermost, non-sticky framework threads. Maximum capture spiral diameter is the length of a straight line extending across a web's center to its outermost capture thread. The dowel rods inside these boxes formed a frame with inner dimensions of  $29.0 \times 21.5$  cm, although some spiders attached their threads to the walls of boxes and, therefore, perceived the space available for web construction as 1–2 cm greater than this. The mean web diameters for *S. referena* was 11.7 cm ( $n = 26$ ,  $SE = 0.7$ ) and that for *U. glomosus* was 18.7 cm ( $n = 29$ ,  $SE = 0.5$ ). The maximum capture spiral diameter for *S. referena* was 11.8 cm ( $n = 26$ ,  $SE = 0.7$ ) and for *U. glomosus* was 19.1 cm ( $n = 29$ ,  $SE = 0.5$ ). Thus, the mean web diameter of *S. referena* is 54% and the maximum capture spiral diameter is 54% of the minimum box dimension. For *U. glomosus* these values are 87% and 89%, respectively. Therefore, box size clearly did not restrict the size of *S. referena* webs and probably did not cause *U. glomosus* to construct smaller webs than those found in the field.

To assess the effect of box size on the triangle-webs of *H. cavatus*, I compared the length of the second radius (the top of the web being the first of four radii) in webs constructed by adult females in the field with those constructed in the laboratory. The length of this radius is highly correlated to other web parameters (Opell unpubl. data) and is, therefore, a good index of web size. The mean length of the second radius in webs constructed in the field was 11.1 cm ( $n = 19$ ,  $SE = 0.7$ ) and that for webs constructed in the laboratory was 14.3 cm ( $n = 30$ ,  $SE = 0.5$ ). The values for both populations were normally distributed (Shapiro-Wilk W-statistic  $P > 0.45$ ) and a  $t$ -test showed that their means were different ( $t = 3.928$ ,  $P < 0.001$ ). This indicates that the structural spacing that *H. cavatus* typically encounters in the field limits the size of its web to a greater degree than

that provided in the laboratory. Consequently, webs constructed in the laboratory may be considered to be of optimal size.

From enlarged photographic prints I counted the number of radii and spirals in each web and measured the web's area with a digitizing tablet. There are two measurements of web area that can be taken: total area, the area inscribed by a web's frame lines, and capture area, the area between a web's outermost and innermost capture spirals. I measured total web area because it seemed a better index of web size for comparisons of web architecture, whereas capture area seems more appropriate for assessing a web's prey capture potential. Craig (1987b) does not report total web area, but does give the mean radius length for each species she studied. I used these data to compute the total area of each species' web as if it were a circle.

**Thread diameters.**—The diameters of uloborid axial fibers are taken from table 2 in Opell (1996). For cribellar threads, two axial fibers were measured per web. This approach assumes that axial fiber diameter is uniform within a web and does not address the possibility that axial fiber diameter changes during the course of capture spiral production. The cribellar fibrils of these threads help hold their axial fibers apart, allowing the diameter of a single fiber to be measured under a transmission electron microscope. The total axial fiber cross sectional area of these cribellar threads was computed as the sum of the cross sectional areas of their two fibers. In contrast, even the interdroplet regions of araneoid capture threads are coated by a thin layer of viscous material. Although the water in this material evaporates under the high vacuum of an electron microscope, it leaves a thin, electron-dense residue that coats the axial fibers, making them appear as a single strand, whose individual fibers cannot be distinguished under either the scanning or transmission electron microscope (Craig 1987b; Opell unpubl. obs.). I computed the combined cross sectional areas of the axial fibers of these threads as the sum of the areas of two circles, each with a diameter of half the capture thread diameter reported by Craig (1987b). This provides a more appropriate estimate of axial fiber cross sectional area than treating the contiguous fibers as if they were a single fiber.

**Statistical analysis.**—The relationships



among spider weight, thread diameter, and web features cannot be determined using traditional regression techniques, as the species included in this study are evolutionarily related, and their values are not strictly independent (Harvey & Pagel 1991). To minimize the effect of phylogenetic position, I employed Huey and Bennett's (1986) method for evaluating the relationships among continuous variables whose states are hypothesized to be functionally linked. This method has three steps: 1) the state of each character in a taxon's most immediate hypothetical ancestor is determined, 2) the change from this ancestral state to the state expressed by extant members is computed for each character, and 3) the relationship between these changes in character states are evaluated by Pearson correlation. If this analysis shows that changes (either positive or negative) in two characters are correlated, then their states can be considered to have coevolved. I determined ancestral values for uloborids and araneoids separately using the unrooted, minimized sum of squared changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison & Maddison 1992). Although this study compares the only uloborids that construct horizontal orb-webs and araneoids that construct vertical orb-webs, *H. cavatus* and *L. globosus* were included in determinations of ancestral values to increase the resolution of these computations.

As spider weight has the potential to affect web features, I used a one way ANOVA to determine if weight differed between: 1) uloborid and araneoid species, 2) uloborids that spin horizontal webs and araneoids that spin vertical webs, 3) uloborid and araneoid species that produce horizontal webs and those that produce vertical webs. These tests showed no differences in spider weight that would compromise this study's findings ( $f = 0.95$ – $1.12$ ,  $P = 0.32$ – $0.36$ ).

## RESULTS

**Values and their normality.**—Because all values or their natural logs are normally distributed, parametric statistics were used in their analysis. Tables 1 and 2 give values for uloborid and araneoid species and Table 3 presents the ancestral values used in transformational analyses. A Shapiro-Wilk W-statistic test of normality showed that changes in axial

fiber cross sectional area, the number of radii per web area, the number of spirals per web area, and in the number of radii per spiral turn were normally distributed ( $P > 0.28$ ) for both the four uloborid species that constructed horizontal webs and the four araneoid species that constructed vertical webs. Change in spider weight was not normally distributed ( $P = 0.002$ ) and the normality of change in web area was questionable ( $P = 0.059$ ). However, changes in the natural logs of these two latter values were normally distributed ( $P > 0.48$ ) for both the four orb-weaving uloborids and the four araneoid orb-weavers that constructed horizontal orb-webs. The number of radii per spiral turn and the weight-specific cross sectional area of axial fibers (Table 5) were normally distributed (Shapiro-Wilk W-statistic  $P > 0.30$ ) for both deinopoid and araneoid clades.

**Correlation between features.**—Five features were shown by Pearson correlation to be significantly correlated for at least one group of orb-weavers (Table 4). Given the small sample size for each clade of spiders and the high correlation values obtained in these analyses, I accept as significant correlations with  $P < 0.10$ . For both cribellate and adhesive orb-weavers spider weight and web area are positively correlated, as are the number of radii per web area and the number of spirals per web area. However, the transition from cribellate to adhesive orbs appears to have been associated with three changes: 1) the gain of a positive relationship between spider weight and capture thread cross sectional area, 2) the loss of a negative relationship between spider weight and the number of spirals per web area, and 3) the loss of a positive relationship between web cross sectional area and the number of radii per spiral turn.

**Differences between uloborid and araneoid orb-webs.**—Both the number of radii per spiral turn and the weight-specific cross sectional area of axial fibers differed between uloborids with horizontal orb-webs and araneoids with vertical orb-webs (Table 5). The number of radii per spiral turn was greater in uloborid orb-webs and the weight-specific axial fiber cross sectional area was greater in araneoid orb-webs.

## DISCUSSION

**Common web features.**—Two architectural relationships appear to be plesiomorphic for

Table 1.—Features of the webs and threads of five species of Uloboridae. Mean  $\pm$  2 standard errors, sample size. Weights are those of individuals whose web features were measured. \*Although many webs constructed by these two species are essentially horizontal, some are constructed at angles of up to about 45°.

	<i>Waitkera waitakerensis</i>	<i>Siratoba referena</i>	<i>Uloborus glomosus</i>	<i>Octonoba sinensis</i>	<i>Hyptiotes cavatus</i>
Web orientation	horizontal	horizontal*	horizontal	horizontal*	vertical
Weight (mg)	7.84 $\pm$ 0.70 <i>n</i> = 32	3.93 $\pm$ 0.44 <i>n</i> = 26	7.16 $\pm$ 0.76 <i>n</i> = 29	12.16 $\pm$ 1.58 <i>n</i> = 24	8.41 $\pm$ 1.22 <i>n</i> = 30
Axial fiber:					
diameter (nm)	236 $\pm$ 44 <i>n</i> = 6	292 $\pm$ 70 <i>n</i> = 5	307 $\pm$ 46 <i>n</i> = 5	340 $\pm$ 30 <i>n</i> = 17	419 $\pm$ 22 <i>n</i> = 17
cross sectional area $\times$ 2 ( $\mu\text{m}^2$ )	0.09 $\pm$ 0.04 <i>n</i> = 6	0.14 $\pm$ 0.06 <i>n</i> = 5	0.15 $\pm$ 0.04 <i>n</i> = 5	0.19 $\pm$ 0.04 <i>n</i> = 17	0.28 $\pm$ 0.02 <i>n</i> = 15
weight-specific area ( $\mu\text{m}^2/\text{mg} \times 10^{-3}$ )	19 $\pm$ 28 <i>n</i> = 6	31 $\pm$ 13 <i>n</i> = 3	21 $\pm$ 6 <i>n</i> = 5	15 $\pm$ 4 <i>n</i> = 16	40 $\pm$ 6 <i>n</i> = 15
web area ( $\text{cm}^2$ )	177 $\pm$ 28 <i>n</i> = 32	109 $\pm$ 26 <i>n</i> = 26	289 $\pm$ 32 <i>n</i> = 29	642 $\pm$ 100 <i>n</i> = 24	155 $\pm$ 16 <i>n</i> = 30
Radii:					
length	4.0 $\pm$ 0.4 <i>n</i> = 25	3.0 $\pm$ 0.5 <i>n</i> = 23	6.3 $\pm$ 0.5 <i>n</i> = 27	8.8 $\pm$ 0.8 <i>n</i> = 24	— —
number	27 $\pm$ 2 <i>n</i> = 32	35 $\pm$ 2 <i>n</i> = 26	34 $\pm$ 2 <i>n</i> = 29	50 $\pm$ 2 <i>n</i> = 24	4 $\pm$ 0 <i>n</i> = 30
number/area	0.17 $\pm$ 0.02 <i>n</i> = 32	0.42 $\pm$ 0.08 <i>n</i> = 26	0.12 $\pm$ 0.02 <i>n</i> = 29	0.9 $\pm$ 0.02 <i>n</i> = 24	0.33 $\pm$ 0.02 <i>n</i> = 30
Capture thread spirals:					
number	12 $\pm$ 2 <i>n</i> = 32	14 $\pm$ 2 <i>n</i> = 26	13 $\pm$ 2 <i>n</i> = 29	17 $\pm$ 2 <i>n</i> = 24	16 $\pm$ 2 <i>n</i> = 30
number/area	0.07 $\pm$ 0.00 <i>n</i> = 32	0.15 $\pm$ 0.02 <i>n</i> = 26	0.5 $\pm$ 0.00 <i>n</i> = 29	0.3 $\pm$ 0.00 <i>n</i> = 24	0.11 $\pm$ 0.02 <i>n</i> = 30
radii/spiral turn	2.37 $\pm$ 0.14 <i>n</i> = 32	2.64 $\pm$ 0.20 <i>n</i> = 26	2.77 $\pm$ 0.22 <i>n</i> = 29	2.98 $\pm$ 0.24 <i>n</i> = 24	0.12 $\pm$ 0.02 <i>n</i> = 30

orb-weaving spiders by virtue of their presence in both deinopoid and araneoid orb-weavers. Both clades exhibit a positive relationships between spider weight and web area and between the number of radii per web area and the number of spirals per web area (Table 4).

The positive relationship between spider weight and web area in both clades shows that this relationship plays an important role in the foraging dynamics of orb-weaving spiders. As spider weight is directly related to metabolic rate (Anderson & Prestwich 1982) and as web size is directly related to prey capture (Brown 1981), this relationship indicates that an orb-web's ability to capture prey tends to scale to a spider's metabolic needs. However, it is im-

portant to note that other factors may also affect web performance. These include prey availability in the microhabitat where a web is placed (Riechert & Cady 1983; Wise & Barata 1983; Craig et al. 1994), web and spider visibility to insects (Craig 1988, 1990; Craig & Bernard 1990; Craig & Ebert 1994; Craig & Freeman 1991), web orientation (Chacón & Eberhard 1980; Eberhard 1989), the ability of a web to absorb the force of an insect strike, web stickiness (Craig 1987b; Eberhard 1986, 1989), spider response time (Eberhard 1989), and the presence of other orb-weaving species (Spiller 1984).

An interspecific comparison of uloborid species (Opell 1996) showed a direct relationship between spider weight and web area, but



Table 2.—Features of the webs and threads of five araneoid species, as given by Craig (1987a, b). Mean  $\pm$  2 standard errors, sample size. \*No variance was provided, as indices were computed from species means.

	<i>Mangora pia</i>	<i>Cyclosa caroli</i>	<i>Micrathena schreibersi</i>	<i>Leucauge globosa</i>	<i>Epilineutes globosus</i>
Web orientation	vertical	vertical	vertical	horizontal	vertical
Weight (mg)	21.2	5.3	146	2.7	0.8
Axial fibers of capture thread:					
diameter (nm)	1900	1038	3040	760	350
cross sectional area ( $\mu\text{m}^2$ )	1.42	0.42	3.63	0.23	0.05
weight-specific area ( $\mu\text{m}^2/\text{mg} \times 10^{-3}$ )	67	79	25	85	63
Web area ( $\text{cm}^2$ )	$216 \pm 0.7$ $n = 42$	$150 \pm 0.5$ $n = 22$	$347 \pm 1.9$ $n = 16$	$125 \pm 0.7$ $n = 16$	$61 \pm 1.7$ $n = 33$
Radius length (cm)	$8.3 \pm 0.68$ $n = 42$	$6.9 \pm 0.56$ $n = 22$	$10.5 \pm 1.10$ $n = 16$	$6.3 \pm 0.66$ $n = 16$	$4.4 \pm 1.14$ $n = 33$
Radii/web area	0.24*	$0.32 \pm 0.06$ $n = 22$	$0.13 \pm 0.02$ $n = 16$	$0.15 \pm 0.02$ $n = 16$	0.06*
Capture spirals/web area	0.25*	$0.30 \pm 0.20$ $n = 10$	$0.09 \pm 0.02$ $n = 9$	$0.18 \pm 0.04$ $n = 8$	0.10*
Radii/spiral turn	2.20*	1.10*	1.40*	0.83*	0.11*

studies of araneoids lead to contradictory conclusions. The latter situation may be explained by the fact that these studies are a mix of intraspecific and interspecific comparisons and that the results of interspecific studies were not analyzed in a phylogenetic context. Risch (1977) measured the weights and spiral areas (area encompassed by the web's inner- and outer-most spiral turn) of juveniles and adult females of four araneid species. His data do not show a strong relationship between these variables, although the species he studied were more similar in weight than the araneoid species included in the current study. Several intraspecific comparisons of the size of adult female araneoids and the size of their webs

show that larger or heavier spiders tend to construct larger webs (Eberhard 1988; Witt et al. 1968), one found no such association in two species (Brown 1981), and another found that adding weights to adults reduced the length of thread in their webs (Christensen et al. 1962). These studies and those of the effect of silk supply, and, by implication, spider nutrition, on web size (Eberhard 1988) demonstrate that web size is plastic and document some of the proximate factors that influence this parameter. Phylogenetic comparisons, like those presented in this study, provide a complementary perspective by documenting ultimate factors that influence orb-web architecture.

Table 3.—Ancestral values used in transformational analyses. The position of these six nodes is given in Figure 1.

	Node 1	Node 2	Node 3	Node 4	Node 5	Node 6
Weight (mg)	7.83	9.76	9.96	33.4	61.6	6.9
Total area of						
axial fibers ( $\mu\text{m}^2$ )	0.21	0.21	0.29	1.29	1.78	0.31
Web area ( $\text{cm}^2$ )	160	396	248	208	235	120
Radius length (cm)	4.3	7.0	—	7.7	8.4	5.7
Radii/area	0.28	0.15	0.24	0.22	0.22	0.14
Spirals/area	0.11	0.06	0.09	0.14	0.18	0.14
Radii/spiral	2.23	2.38	1.40	1.68	1.39	0.96

Table 4.—Comparison of the relationships found among four cribellate orb-weaving species and four adhesive orb-weaving species using Pearson correlation. Significant values ( $P < 0.10$ ) are indicated by an asterisk (\*).

	Horizontal, cribellate orb-webs	Vertical, adhesive orb-webs
Change in $L_n$ weight and in $L_n$ web area	$r = 0.94^*$ $P = 0.056^*$	$r = 0.96^*$ $P = 0.038^*$
Change in radii per web area and in spirals per web area	$r = 0.99^*$ $P = 0.007^*$	$r = 0.91^*$ $P = 0.092^*$
Change in $L_n$ weight and in spirals per web area	$r = -0.92^*$ $P = 0.078^*$	$r = -0.75$ $P = 0.254$
Change in axial fiber cross sectional area and in radii per spiral turn	$r = 1.00^*$ $P = 0.001^*$	$r = 0.37$ $P = 0.634$
Change in $L_n$ weight and in $L_n$ axial fiber cross sectional area	$r = 0.16$ $P = 0.844$	$r = 0.94^*$ $P = 0.062^*$

The positive relationship between the number of radii per web area and the number of spirals per web area factors out web area and, therefore, reflects a positive relationship between the number of radii and the number of spirals in a web. This relationship has been noted by Eberhard (1972, 1986), who concluded that, although there are exceptions, the number of radii and spiral turns “are about equal”. Although the current study is based on only nine orb-weaving species, it suggests that orb-webs tend to have more radii than spirals. The webs of the nine orb-weaving species studied had a mean radii per spiral turn ratio of 1.88. However, this study included four species of the family Uloboridae, a group that Eberhard (1986) considers to have a greater than typical number of radii. When these uloborid species are excluded, the mean ratio drops to 1.23 radii per spiral turn. Among araneoids, the number of radii decrease as spiders develop (Risch 1977; Wiehle 1927; Witt et al. 1968). This may indicate that

larger araneoid species tend to have fewer radii in their webs than do smaller species. However, as only one very large araneoid species was included in the current study, size alone cannot account for the lower radii per spiral turn ratio in araneoid webs (Table 5).

**Differences in cribellate to adhesive orb-web.**—The evolution of the Araneoidea was associated with a shift from horizontal orb-webs that contained cribellar capture threads to vertical orb-webs that contained adhesive capture threads (Bond & Opell pers. obs.). The vertical orientation of araneoid orb-webs subjects them to greater forces of prey impact than does the horizontal orientation of uloborid orb-webs (Craig 1987a; Eberhard 1989). This kinetic energy is absorbed in two major ways: some is borne by the web’s radii and frame threads and some is dissipated by aerodynamic damping as the web extends and its capture threads resist movement through the air (Lin et al. 1995).

The greater weight-specific cross sectional

Table 5.—Comparison of two web features in uloborid and araneoid orb-webs. Mean  $\pm$  2 standard errors. Below the name of each index appears the results of a  $t$ -test.

	Uloborid species with horizontal orb-webs ( $n = 4$ )	Araneoid species with vertical orb-webs ( $n = 4$ )
Radii/spiral turn ( $t = 3.30$ , $P = 0.016$ )	$2.69 \pm 0.26$	$1.20 \pm 0.86$
Weight-specific axial fiber cross sectional area $\mu\text{m}^2/\text{mg} \times 10^{-3}$ ( $t = 3.04$ , $P = 0.023$ )	$22 \pm 7$	$59 \pm 23$



areas of araneoid axial fibers (Table 5) indicate that these adhesive capture threads are stronger than those constructed by uloborids and, thus, better adapted to transfer greater forces to the web's stronger radial threads. For the five araneoid species, there is a positive relationship (Pearson  $r = 0.97$ ,  $P = 0.007$ ) between the total axial fiber cross sectional area computed in this study and the capture thread tensile strength reported by Craig (1987a). As the axial fibers of cribellar and adhesive capture threads are homologous, the cross sectional area of axial fibers in cribellar thread is probably also a good index of thread tensile strength. Although the spectral properties of light reflected by cribellar and adhesive threads differ (Craig & Bernard 1990), these measurements include the non-homologous cribellar fibril and adhesive material that covers the axial fibers. Therefore, these differences do not necessarily show that the protein composition of the axial fibers of these threads differs.

Architectural differences between uloborid and araneoid orb-webs suggest that their functional dynamics also differ. Radius-rich webs, like those constructed by uloborids (Table 5), tend to be stiff and radius-poor webs, like those constructed by araneoids, tend to be more extensible (Craig 1987b). The study of Lin et al. (1995) suggests that the more extensible a web is, the more kinetic energy it is able to dissipate through aerodynamic dampening. Therefore, the greater extensibility of adhesive capture threads (Vollrath & Edmonds 1989; Köhler and Vollrath 1995) may enhance aerodynamic dampening by increasing overall web extensibility. The greater extensibility of adhesive capture thread may also serve to dissipate some force in the immediate area of a prey strike before transferring the remanding force to adjacent threads.

Additional evidence that the replacement of cribellar threads by adhesive threads changes web dynamics comes from a comparison of vertical and horizontal adhesive orb-webs. If differences between uloborid and araneoid orb-webs are associated principally with differences in web orientation, then they should also be observed when horizontal and vertical adhesive orb-webs are compared. However, Craig's (1987a) data suggest that horizontal araneoid orb-webs have fewer, not more, radii per spiral turns than vertical araneoid orb-

webs. This is contrary to the difference between horizontal uloborid and vertical araneoid orb-webs observed in this study and suggests that the replacement of cribellar threads by adhesive threads may also enhance a web's ability to dissipate the force of a prey strike. It may also indicate that the radial threads of araneoid orb-webs are stronger than those of deinopoid orb-webs, either because they have greater diameters or different silk composition.

The lower radius-to-capture-spiral ratio of araneoid orb-webs may also contribute to the positive relationship between spider weight and axial fiber cross sectional area that characterizes vertical araneoid orb-webs (Table 4; Craig 1987a). As capture threads become a more prominent component of the vertical araneoid orb-web, they play a greater role in transferring force to the web's stiffer radial threads (Lin et al. 1995) and must be strong enough to withstand this force. However, there appears to be a limit on the amount of material that an orb-weaving spider can devote to capture thread production (Eberhard 1972, 1989; Peters 1937; Witt et al. 1968). As the total volume of adhesive capture thread in a spider's web is directly related to spider weight (Opell unpubl. obs.), axial fiber diameter may ultimately be determined by the competing requirements that a spider must produce a length of capture thread that is long enough and sticky enough to capture sufficient prey and strong enough to withstand the force of prey impact. As a spider's weight affects both its metabolic demand (Anderson & Prestwich 1982) and total thread volume, it is not surprising that the cross sectional area of araneoid axial fibers is related to spider weight.

In uloborids, the cross sectional area of capture thread axial fibers is not related to spider weight, but instead to the maximum distance that a capture thread spans in the web (Opell 1994d). This difference and the smaller weight-specific axial fiber cross sectional areas of cribellar threads suggest that different factors influence axial fibers of uloborids and araneoids. The lower forces of prey impact that uloborid webs typically experience may not require the axial fibers of their capture threads to be as strong. Additionally, as in araneoids, the volume of material that these spiders can devote to capture thread production appears to be limited (Eberhard 1972). There-



fore the large amount of silk volume that uloborids must devote to the cribellar fibrils of their capture threads to achieve thread stickiness (Opell 1994b, 1996) may indirectly restrict that amount of silk that can be expended as axial fibers.

Cribellate orb-webs are characterized by a negative relationship between spider weight and the number of spirals per web area and by a positive relationship between axial fiber cross sectional area and the number of radii per spiral turn. Neither relationship is present in araneoids. The first relationship indicates that spiral spacing increases as spider size increases. Spiral spacing may be more highly constrained in uloborids because the webs that these spiders construct appear to be less well equipped than araneoid orb-webs to retain prey and because uloborids are less well equipped than araneoids to subdue intercepted prey. Not only do horizontal webs retain prey for shorter periods of time than vertical webs with threads of the same stickiness (Eberhard 1989); but, relative to the weight of the spider that produced them, cribellar capture threads are less sticky than adhesive threads (Opell unpubl. obs.). Additionally, uloborids lack poison glands and must rely entirely on silk wrapping to quiet prey and prevent their escape from the web (Lubin 1986; Opell 1979). As orb-webs trap prey more efficiently when capture spiral spacing exceeds prey diameter (Chacón & Eberhard 1980; Eberhard 1986), the more closely spaced spirals of orb-webs constructed by small uloborid species may be particularly important in equipping these webs to intercept prey that they can retain and that spiders can subdue. The greater stickiness of adhesive capture threads (Opell unpubl. obs.) may further increase the prey capture efficiency of vertical araneoid orb-webs and allow their spiral spacing more latitude to differ in ways that adapt webs to a particular habitat or prey type.

In uloborids, but not in araneoids, axial fiber cross sectional area increases as the number of radii per spiral turn increases. In view of the positive relationship between the number of radii per web area and the number of spiral turns per web area, this indicates that increased axial fiber cross sectional area adds to overall web strength by complementing an increase in the number of radii rather than by compensating for a decrease in the relative

number of spiral turns. The lower extensibility of cribellar threads (Köhler & Vollrath 1995) and the stiffer, radius-rich webs of uloborids (Table 5) may help explain why the cross sectional areas of their capture threads responds to this change in web architecture and those of araneoids do not. If uloborid orb-webs have a lower ability to dissipate force through extension and aerial dampening, they may meet this challenge by becoming stronger. If the axial fibers' chemical structure is unchanged, then increased strength is gained by increased cross sectional area.

**Conclusions.**—Orb-webs constructed by members of the deinopoid and araneoid clades share many features, including an area that is related to spider weight. However, this study shows that there are important architectural differences between the webs that are spun by members of these sister clades. The functional implications of these differences are consistent with the observation that vertical araneoid orb-webs typically experience greater forces of prey impact than do deinopoid orb-webs. Compared to horizontal orb-webs, the vertical orb-webs of araneoids appear to have stronger capture thread axial fibers and to be better equipped to implement aerodynamic dampening by virtue of their lower radius-to-spiral ratio. The greater extensibility of adhesive capture thread may contribute in a minor way to overall web extensibility and force dissipation, but the model of orb-web dynamics developed by Lin et al. (1995) suggest that it does not play a major role. Therefore, the selective advantage of adhesive capture thread over cribellar capture thread may be due principally to the greater economy and greater stickiness of adhesive thread (Opell unpubl. data) and to its reduced ultra violet reflectance (Craig & Bernard 1990) that makes it less visible to insects and allows araneoid orb-weavers to occupy an expanded range of microhabitats (Craig et al. 1994).

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## NATURAL HISTORY AND COPULATORY BEHAVIOR OF THE SPINY ORBWEAVING SPIDER *MICRATHENA GRACILIS* (ARANEAE, ARANEIDAE)

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**ABSTRACT.** We examine copulatory behavior and the reproductive natural history of the spiny orb-weaver, *Micrathena gracilis*. Censuses were conducted on free-ranging, individually marked spiders. After molting to adulthood, males induct sperm into their palps and then search for mates. Females inhabit solitary, individually-constructed webs. Males preferentially remain with penultimate-instar females, those about to molt and mate for the first time. After a female molts and constructs a viscid spiral, males build mating threads on which they court. After copulating, the male must dismount and reapproach the female to inseminate her second reproductive tract. Two copulations are therefore required for a complete mating between male and female. Some males, however, obtained only one copulation and two males often copulated with a given female. Staged encounters in the field revealed the important observation that when a male did copulate twice with a female, the duration of the second copulation was more than twice as long as the first. Shortly after the second copulation, the male inducted sperm into the palps and moved away. Females remained sexually receptive throughout their lives and apparently mated with any male. Females oviposited about 30 days after molting and mating. Egg sacs were cryptic in appearance and yet clutch mortality was high. Copulatory behavior is discussed in relation to this reproductive natural history.

Spiders offer an intriguing model for the study of reproduction. To begin, the sexes often differ dramatically in both morphology and behavior (Foelix 1980; Vollrath & Parker 1992). The female orbweaver, for example, is generally a relatively large, sedentary predator while the adult male is smaller and, at least as an adult, a wanderer. The shape and presence and arrangement of sperm intake and fertilization ducts of the female spider's reproductive tracts is thought to have a strong influence on male sexual maturation rates and the pattern of cohabitation with females. Conduit spermathecae, those with separate insemination and fertilization ducts (entelegynes), are thought to promote a first male advantage in fertilization due to a serial ordering of sperm and a first-in/first-out usage pattern (Austad 1984). Consequently, males of such species usually mature before females and cohabit with penultimate-instar females approaching the final molt and sexual maturity (Christenson & Goist 1979; Robinson & Robinson 1980; Jackson 1986; Watson 1990; Dodson & Beck 1993). Cul-de-sac spermathecae, those with common insemination and fertilization ducts (haplogynes), are thought to

promote a last male advantage because the sperm from the last mating are nearer to the exit of the duct and a last-in/first-out usage pattern (Austad 1984). This is supported by Kastner & Jacobs (1997; but see Eberhard et al. 1993). In this case there should be no selective pressure for early male maturation and preferential cohabitation with females approaching sexual maturity. Males mature at about the same time or after females and cohabitation with juvenile females is not noted (Huff & Coyle 1992; Eberhard et al. 1993)

While the morphology of the female reproductive tract may influence male advantage patterns for fertilization of a female's eggs, sexual maturation rates and male cohabitation patterns, the relationship between the female's reproductive tract morphology and copulatory behavior is uncertain. It is known that males of species with cul-de-sac spermathecae often simultaneously insert both palps during copulation (Foelix 1980). The patterns of palpal insertion and duration of copulation among species with conduit spermathecae show extreme variability within and between species (Robinson & Robinson 1980; Elgar 1995). Males can insert one palp several times before

switching to the opposite palp or insert each palp once. Perhaps features of the natural history can influence, or at least help explain, male reproductive behaviors.

Our work focuses on the natural history and copulatory behavior in the spiny orbweaving spider, *Micrathena gracilis* (Walckenaer 1805). The genus *Micrathena* Sundevall 1833 contains over 100 species distributed throughout the New World tropics, with three found in North America (Levi 1978, 1985). The two species native to Louisiana, *M. gracilis* and *M. sagittata* (Walckenaer 1841), have one generation a year at our study site. *Micrathena* are characterized by prominent spines on the female abdomen. The male is only a fraction of the size of the female with little similarity in form. Female *Micrathena* are also entelegynes, having separate insemination and fertilization ducts (Levi 1978, 1985). Limited observations of mating in captive *M. gracilis* were recorded by Montgomery (1903). Observations have also been conducted on *M. gracilis* macrohabitat preferences (Hodge 1987a), site tenacity (Hodge 1987b) and prey selection (Uetz & Biere 1980; Uetz & Hartsock 1987).

During the course of field observations of *M. gracilis*, we noted that a complete mating between a given male and female entails two copulations (insertions), one for each of the two male and female copulatory organs. After the first copulation, the male must dismount and reapproach the female to copulate again. Staged encounters revealed the important observation that the durations of the two copulations are asymmetrical. As we report here, the duration of the second copulation is more than twice as long as that of the first. Others have noted such differences in copulatory durations (Bristowe 1929; Huber 1993, 1995; Sasaki & Iwahashi 1995); but to our knowledge, no one has yet addressed how a copulatory pattern might be related to a species' natural history.

We conducted a census of marked, unrestrained animals and observed staged encounters to describe copulatory behavior of *M. gracilis* and to place it within a framework of reproductive natural history. We describe the timing of sexual maturation, architecture of the female web, behavior of males on the female web, courtship and copulation, the likelihood that copulation will occur, sperm in-

duction, female oviposition and egg sac mortality. We then discuss how male copulatory pattern may relate to these natural history data.

## METHODS

**Study site.**—Observations were conducted at the F. Edward Hebert Center of Tulane University, 20 km south of New Orleans, Louisiana. The studies were conducted on a 30 × 40 m plot in a hardwood, bottomland forest. *M. gracilis* occur there in relatively large numbers. The study area, located next to a lagoon, is frequently flooded during the spider's mating season.

**Census procedures.**—To describe reproductive natural history, census observations were made during June through September, 1990 and 1991. Census animals were individually marked with fast-drying acrylic paint and were observed daily. Females were marked on the tips of the spines and males on the dorsal surface of the abdomen. When animals molted they were re-marked. Paint-marking had no obvious effects on the spiders' behavior. All web sites were tagged. During the 1990 field season, a total of 143 females was observed between 0700–1600 h; no males were marked. During the 1991 field season, a total of 102 females and 105 males was observed between 0700–1600 h. Each day the census area was thoroughly scanned for animals and all animals were briefly observed at least once. All unmarked animals located in the census area were marked. Noted were the presence of a viscid spiral (prey catching surface) and web support strands, presence and identity of the female and males on a web, pattern of residency, molting, mating, oviposition, and disappearance or movement from the web site. For analyses of male residency on a female's web we used the term "male days". For example, if two males were present on a particular day on a given female's web, we scored this as two male days for that female on that day.

Every other day in late July and August of 1990, two plots about one km apart were searched for new egg sacs. Tagged intact sacs were examined daily. Five sacs were collected mid-season and their clutches were removed and weighed on a Mettler analytical balance. Eggs were then separated from each clutch with a paintbrush and 10 groups of 20 eggs



( $n = 200$  eggs per clutch, most of the eggs in the clutch) were weighed. The length and width of 10 eggs from each clutch were also measured.

**Timing of first sperm induction.**—Five penultimate-instar males approaching the final molt were placed in separate 250 ml collection vials that contained two small twigs. The vials were examined daily for molting or exoskeletons. The date molted was recorded. Three days later the males were brought into the lab and examined for sperm content. The methods for determining sperm content are reported elsewhere (Bukowski & Christenson 1997). Here we simply note whether sperm were present in the palps or not.

**Procedures for staged matings.**—To facilitate the observation of complete mating sequences, we conducted staged encounters between males and females in 1990 and 1991. To be certain females were virgin, they were monitored for an impending molt, which is preceded a day or two by failure to construct a viscid spiral. The abdomen of a penultimate-instar female approaching the final molt is spherical with relatively short spines while that of the newly-molted female is elongate with longer spines. Penultimate-instar females were placed in 250 ml plastic collection vials where they molted to adulthood. This ensured they did not copulate overnight when not observed. The females were released the next day at their original web site. Males were collected from the webs of penultimate-instar females and usually held a couple of days prior to testing. After collection they were examined under a dissecting microscope for bodily damage. Over the 1991 field season, 176 males were also examined for bodily damage to determine if they are typically injured in male-male interactions. The reproductive histories of the males were not known.

Staged encounters were initiated only under dry conditions. Females were released at 0800 h and allowed to build webs. A randomly chosen male was placed on an upper frame thread after the female had constructed the viscid spiral. Copulation is defined as the interval between palpal insertion and male dismount from the female, usually occurring immediately after removal of the palp. The intercopulatory interval refers to the amount of time between an animal's first and second copulation.

**Frequency and duration of copulation.** Males ( $n = 20$ ) were each presented to a female ( $n = 20$ ) and allowed to copulate twice and depart the web. Males were observed until after sperm induction or until  $1\frac{1}{2}$  h had elapsed. Both male and female were then collected and weighed (wet weight) that evening in the laboratory on a Mettler analytical balance. Both males and females were released at the field station the following day.

**Phases of copulation:** We examined in detail the phases (inflation state of the hematochoa) of the two copulations. The males ( $n = 13$ ) used were taken from studies involving other factors that influence frequency and duration of copulation (Bukowski & Christenson unpubl. data). We recorded how long the hematochoae were inflated, the length of time deflating, intervals between deflation and palp removal, and palp removal and dismount.

**Prolonged second copulation:** We tested whether the second copulation would be prolonged when a male ( $n = 15$ ) copulated with one palp with one virgin female and was then given another virgin female.

**Statistics.**—All summary statistics are reported as  $\bar{x} \pm \text{SD}$ .

## RESULTS

**Sexual maturation.**—Mating occurred from mid-June to mid-August. Early in June 1991 all females ( $n = 24$ ) and all ( $n = 19$ ) but one male in the study area were juveniles. By late June, only 10.7% of the females ( $n = 51$ ) had matured compared to more than 70% of males ( $n = 21$ ,  $\chi^2 = 24.97$ ,  $P < 0.00001$ ). Sex ratio appeared to change over time as well. In early June, the ratio was nearly at unity ( $n = 24\text{♀}$ ,  $n = 19\text{♂}$ , 1.3:1;  $\chi^2 = 0.58$ ,  $P = 0.44$ ) and by late June females ( $n = 51$ ) outnumbered males ( $n = 21$ ; 2.4:1;  $\chi^2 = 5.4$ ,  $P = 0.02$ ). Wandering adult males are difficult to find so these numbers represent, for the most part, males on females' webs.

After molting to adulthood, males remained on a single strand of their last web for  $3.0 \pm 1.2$  days ( $n = 22$ ). By this time, the dorsum remained white, but other body parts had turned from a gray to a rusty-red or black. In contrast, females were tan, black and white, or black and appeared not to change color at sexual maturation. Adult males weighed  $3.3 \pm 0.3$  mg ( $n = 20$ ) and newly-molted females

weighed  $45.0 \pm 6.6$  mg ( $n = 20$ ). Adult males appeared not to feed, although they can drink water from leaves or silk surfaces.

**Timing of first sperm induction.**—It is not known when or where free-moving males first induct sperm to the palps. Presumably this is done before they leave their last web site. Males presented to females did not induct sperm prior to mating, but did so after mating (see post-copulatory sperm induction below). However, the best evidence for sperm induction prior to mate searching was found with males that had molted to adulthood in collection vials. Three days after the final molt all males ( $n = 5$ ) had sperm in both palps.

**The female's web.**—After sunrise, females built radially symmetric orbs usually within 4 m of the ground. The web is essentially two-dimensional with a relatively small (about 20 cm in diameter) viscid spiral situated within triangular frame threads and maintained under high tension (Uetz & Hartsock 1987). The viscid spiral is sloped between 0–45° off of vertical. There are no support or barrier strands adjacent to the hub. Females remained at the hub with the head down, abdomen tilted back, and the dorsum parallel to and facing the ground. This is an unusual position made possible by the relatively long fourth femora (see photos and drawings in Levi 1985). At dusk, the female ingested virtually every strand except frame threads, on which she remained until morning.

Two to four days before the final molt, the female removed her viscid spiral and did not construct another until after the molt. Generally, all that remained was the top horizontal support strand and this was usually shortened within a day before the molt. Females would move within 2–3 cm of one end of the strand and there they molted. After shedding the exoskeleton, the top foundation strand was lengthened and used as a foundation thread for the next viscid spiral. The exoskeleton was removed from the molting thread and reconnected on the upper foundation strand near the edge of the viscid spiral. This pattern of molting behavior was similar for juvenile females and males.

Census females in the penultimate instar ( $n = 17$ ) remained at their web sites for  $11.4 \pm 5.8$  days and moved  $0.35 \pm 0.6$  times between the penultimate and final molts. The interval between the penultimate and final molts

Table 1.—Census females: number of census female observation days, number of female observation days with one or more males present, and number of observation days that males were found on the webs of ante-penultimate instar or younger females, penultimate-instar females and adult females. Some individual females are represented in more than one age category.

Female instar	Number of days with at		
	Number of female days	least one male present	Number of male days
≤Ante-penultimate	621	30	38
Penultimate	726	217	297
Adult	174	7	8

was  $15.4 \pm 2.1$  days. Only 29% ever moved during this time. Adult census females ( $n = 81$ ) remained at their web sites for  $19.8 \pm 12.3$  days and moved  $2.2 \pm 1.3$  times before death or disappearance.

**Male residency on females' webs.**—Of 73 individually-marked adult males, 40 were marked the day of their final molt or were found with an exoskeleton. Nearly half of the males ( $n = 19$ ) that were marked the day of their final molt were never found after leaving their tagged sites. Most marked males were found on the web of one ( $n = 28$ ) or two ( $n = 15$ ) females, but some were found on the webs of three ( $n = 8$ ), four ( $n = 2$ ) or seven ( $n = 1$ ). Overall, males were observed to visit  $1.3 \pm 1.25$  females.

Males were more likely found with penultimate-instar than with younger juvenile or non-virgin adult females (Table 1;  $\chi^2 = 170.8$ ,  $P < 0.00001$ ). Over the census period, only 21 males were noted with ante-penultimate females and they stayed  $2.2 \pm 2.1$  days. Seven of those males were present when the female molted to the penultimate instar and all left the web that day. Males ( $n = 80$ ) did not remain significantly longer ( $\bar{x} = 3.3 \pm 2.6$  days) with penultimate-instar than ante-penultimate instar females ( $F_{1,99} = 2.98$ ,  $P = 0.09$ ). Males were infrequently found with adult females; they were always observed *in copula*.

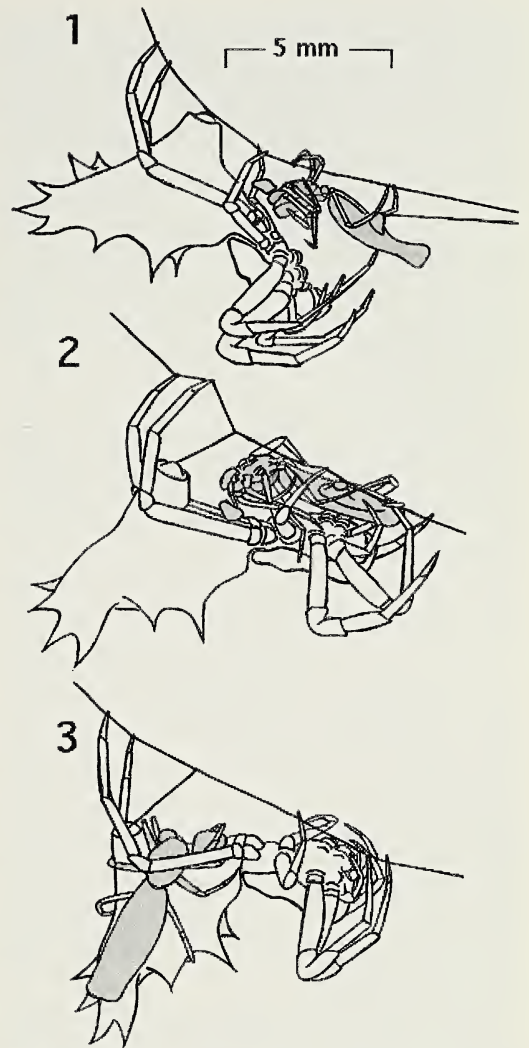
As each female approached her final molt the number of males on her web increased. We sampled three periods of equal length during the penultimate instar: (1) just after the



molt to the penultimate instar, (2) mid-instar, and (3) just prior to the final molt. The duration of each period was not constant across females. The durations of the periods were slightly different for some females and were based (*post hoc*) on the number of days a given female did not construct a viscid spiral prior to the final molt,  $3.6 \pm 1.3$  days. Therefore, the average number of days for each of the three periods is also  $3.6 \pm 1.3$  days. Male presence significantly differed across these three time periods (male days,  $F_{2,32} = 14.8$ ,  $P < 0.0001$ ; number of males,  $F_{2,32} = 21.46$ ,  $P < 0.0001$ ). *Post-hoc* means comparisons showed that male presence increased with each time period. Few males were found with females that had just molted to the penultimate instar ( $0.2 \pm 0.7$  male days,  $0.1 \pm 0.3$  males). A few more males were present at a point midway through the penultimate instar ( $1.5 \pm 2.3$  male days,  $P = 0.056$ ;  $0.6 \pm 0.9$  males,  $P = 0.032$ ). Even more males were found with the female immediately prior to the final molt ( $3.6 \pm 2.9$  male days,  $P = 0.0018$ ;  $1.5 \pm 1.1$  males,  $P = 0.0002$ ).

Of 33 known penultimate-instar census females, 79% ( $n = 26$ ) had at least one male ( $\bar{x} = 1.6$ , range 1–6) present the day before they molted. Males were usually stationary and found near the ends of foundation or peripheral strands. One to two days prior to the final molt, when no viscid spiral was constructed, males seemed to become more active and to be located nearer the female. A detailed description of intermale encounters was difficult to attain with the unaided eye, given male size and speed of engagement. Male encounters might be described as chases with brief physical contact. Males generally maintained all eight legs and examination revealed no signs of bodily damage. Of the 176 adult males collected from the webs of penultimate-instar females (1991) and examined under a dissecting microscope, only five males were missing a leg. Five others were missing a palp.

**Courtship and copulation.**—Just after the female's final molt, when she became sexually receptive, she mated while on a single strand or after she constructed a viscid spiral. In the latter case, the male constructed a mating thread between the end of the primary foundation strand and the outer end of a radial strand. The male courted vigorously by bouncing, bobbing and abdomen wagging, as



Figures 1–3.—Lateral view of copulatory mounting of *Micrathena gracilis*. Male spider is shaded and female spider is white. 1. Female acceptance posture and male approach; 2. Insertion; 3. Final copulatory position. See text for details.

defined for other *Micrathena* species by Robinson & Robinson (1980). The sequence of events leading to insertion and the copulatory position of *M. gracilis* is very similar to that of *M. schreibersi* (Perti 1833), also described by Robinson & Robinson (1980).

When a female at the hub of a viscid spiral responded to a courting male, she moved across the viscid spiral, on the radial strand connected to the male's mating thread. She moved onto the mating thread, and then let go with the first (I), second (II), and sometimes

third (III) pairs of legs (see Fig. 1). If the female were hanging by legs II–IV, the male bit and pulled at legs II until the female released them from the mating thread. This acceptance posture, necessary for coupling, placed the female at the proper angle for insertion, about 40–45° below the horizontal silk strand. The male then moved toward the female so they were head to head. Unsuccessful attempts at insertion were often followed by the male jumping from the female. The male then hung from his dragline, which was connected to the mating thread.

When the male inserted one palp, the female grasped the male's abdomen with legs I and II and chelicerae and appeared to pull him in further toward her epigynum (see Fig. 2). The female then rubbed legs I and II against his ventrum. Through an apparently joint effort, the male was flipped over 180° so that they were positioned ventrum to ventrum and facing essentially the same direction (see Fig. 3). The male was positioned with his cephalothorax midline at the epigynum and his abdomen at an angle of 30–45° to the major axis of the female's abdomen. A male that was positioned over the female's left side had the right palp inserted into the female's right genital pore. The male's body was bent at the pedicel, following the contour of the female's body. The male was connected by a thread to the female's abdomen which was later used when dismounting.

Once inserted and flipped over onto the female's abdomen, the male was firmly locked in place. Shortly after being properly positioned, the hematodocha expanded to full size. As with females of many *Micrathena* species, *M. gracilis* females have an epigynal protuberance (scape) oriented just below and medial to the spermathecae (Levi 1985). During copulation, the male's hematodocha nearly surrounded the end of this structure. Sclerotized parts of the palp closely gripped the scape at defined indentations. No contractions or changes in the hematodocha could be seen with the unaided eye and neither males nor females showed rhythmic movements while *in copula*.

After copulation was initiated, the female returned to the hub. The female's mobility was not compromised and she was able to capture and feed on prey items while mating. Within a few minutes the hematodocha deflated and

within a few seconds the male removed the palp from the female's copulatory pore. Occasionally a male would begin pulling at the engaged palp at about the time most males would dismount. If the palp were not removed immediately, the male usually remained inserted for a relatively long period, apparently stuck. On a few rare occasions free-moving females in the field were noted with a dismembered palp in the epigynum.

Complete insemination of the female requires two distinct copulations. Due to the specific orientation required for insertion, males must dismount the female in order to re-mount and copulate a second time. Thus, once mounted, males intromit and copulate once with one palp and can inseminate only one spermatheca during that mount.

If more than one male were present with a receptive female, they would sometimes sever one another's mating threads, occasionally causing a male to fall from the web (Bukowski & Christenson unpubl. data). If one was engaged in copulation, another would often court, causing the female to move out onto his mating thread and exhibit the acceptance posture. This male would approach and attempt insertion which was precluded by the position of the copulating male. It then bit at the legs and palps of the engaged male but never dislodged it. A few males severed web foundation strands, causing the web to collapse.

**Method of dismounting the female.**—At the termination of copulation, the male ( $n = 19$ ) either climbed ( $n = 10$ ) off the female and moved up across the viscid spiral to the top frame thread or it jumped ( $n = 9$ ) off and hung below the web, connected to her abdomen by the dismount thread. Movement of males opting for the former tactic elicited vigorous jerking and pursuit by the female. After reaching a foundation strand, the male would immediately construct a mating thread and court. During staged encounters, the intercopulatory interval for males that climbed was  $203 \pm 241$  sec ( $n = 9$ ).

Males that jumped off occasionally attempted to climb back up the dismounting strand. The female usually jerked her abdomen vigorously, breaking the dismount strand and disconnecting the pair. Those that remained suspended released silk that usually connected to the bottom foundation strand or to nearby veg-



etation. If the released silk did not connect to the web, the male sent out additional strands until one attached. If several attempts failed, the male moved away from the web. Once the released silk connected, the male climbed onto the foundation strand, constructed a mating thread, and courted. During staged encounters, the intercopulatory interval for males that jumped ( $440 \pm 278$  sec,  $n = 6$ ) was not significantly shorter than for males that climbed ( $203 \pm 241$  sec,  $n = 9$ ,  $F_{1,13} = 3.1$ ,  $P = 0.10$ ). However, one male that climbed off the female courted the female nearly immediately, but was not able to insert until 834 sec later. When this outlier is removed, the intercopulatory interval for males that climbed ( $123.4 \pm 49$  sec,  $n = 5$ ) was significantly shorter than for males that jumped ( $F_{1,12} = 10.23$ ,  $P = 0.008$ ). Males did not groom legs or palps between copulations. The likelihood of obtaining a second copulation did not differ for males that climbed or jumped ( $\chi^2 = 0.72$ ,  $P = 0.40$ ).

**Frequency of re-mating.**—Females were sexually receptive throughout their lives and mated with virtually any male that encountered her web. Of the 57 adult census females (1990) that were observed briefly each day until oviposition, 34 (60%) were observed to mate on the day of the final molt, generally within 1 h after the molt. An additional 23 were observed to re-mate at a later date; 15 did so at least once, three twice, four thrice and one five times. Newly-molted females often alternated copulations with two or more males. Overall, census females were observed to mate with  $1.7 \pm 1.1$  males. The frequency of female mating is likely to be much higher, however, because copulations are brief and males do not remain after mating.

**Copulations during staged encounters.**—Staged encounters were held to determine more accurately the likelihood and duration of copulation under more controlled conditions.

**Frequency and duration of copulation:** Of the 20 newly-molted females presented a male, 19 were receptive. Fifteen (78.9%) copulated with the male on both sides or reproductive tracts, while four (21.1%) copulated on only one side. Of these four females, one did not respond to the male's courtship after the first copulation, one had a male possessing only one palp (the male pulled the other palp off after it was examined under the micro-

scope and before it copulated) and he did not court a second time; and the other two males jumped after the first copulation and became disconnected. The female that did not copulate was presented a total of four males. She severed their mating threads or bit and threw the males to the ground.

For the second copulation, males employed the unused palp and inserted it into the virgin epigynal opening. All males ( $n = 15$ ) copulated for a longer duration during the second coupling ( $1448 \pm 1265$  sec) than the first ( $630 \pm 178$  sec,  $F_{1,14} = 5.93$ ,  $P = 0.029$ ). The copulatory duration for males that mated on one side only ( $548 \pm 232$  sec,  $n = 4$ ) did not significantly differ from the duration of the first copulation of males that mated on both sides ( $F_{1,17} = 0.56$ ,  $P = 0.46$ ). All males terminated the second copulation by jumping off the female and hanging by the dismount strand. After mating, males departed the web, thus post-mate defense was not noted.

**Phases of copulation:** We examined in detail the inflation phases of copulations of an additional group of males ( $n = 13$ ). Once the palpal conductor was inserted, the hematodochae inflated, reaching full size (several times larger than the unused palp) by the end of the first minute. At this time the hematodochae appeared a translucent tan color. After several minutes (see Table 2 for time course of copulatory events), the hematodocha turned opaque white as it began deflating. The conductor remained inserted for a few minutes after deflation. It was then removed and the male dismounted. Overall, the second copulation was significantly longer than the first ( $F_{1,12} = 30.17$ ,  $P < 0.0001$ ; Table 2). Significantly different amounts of time were spent in each phase within a copulation ( $F_{3,36} = 29.99$ ,  $P < 0.0001$ ); most of the copulatory time was spent with the hematodochae inflated and less time was spent in each successive phase. The copulation (first or second) by phase (the four phases) interaction was significant ( $F_{3,36} = 3.06$ ,  $P = 0.041$ ); while the duration of the inflation phase was twice as long in the second copulation, the time taken for deflation and the time from deflation to palp removal showed a five and eight-fold increase, respectively, in the second copulation (Table 2).

Longer hematodochal inflation time did not necessarily result in a longer time to deflate.

Table 2.—Mean durations (seconds) of copulatory phases and mean copulatory durations for the first and second copulations with newly-molted virgin females ( $n = 13$ ).

	First copulation		Second copulation	
	Mean	SD	Mean	SD
Duration of hematochochal inflation	507	127	1036	508
Duration of hematochochal deflation	95	86	408	454
End of deflation to palp removal	61	60	429	505
Palp removal to dismount	6	9	28	31
Total copulatory duration	670	201	1898	862

There were no significant relationships between the duration of hematochochal inflation and the amount of time taken to deflate for the first ( $r = +0.29$ ,  $P = 0.33$ ) or the second copulation ( $r = +0.05$ ,  $P = 0.88$ ). There was no significant relationship between the durations of the first and the second copulations for males copulating twice ( $r = +0.09$ ,  $P = 0.63$ ,  $n = 28$ ). However, one male's palp became stuck in the female during the second copulation and he could not remove the palp until 5684 sec. When data on this male are removed, there was a significant positive relationship between the duration of the first and second copulation ( $r = +0.44$ ,  $P = 0.02$ ; Fig. 4).

We examined the distributions of the durations of the first and second copulations for all animals that copulated twice with a single female ( $n = 28$ ). We followed the method used by Suter (1990) to examine copulatory

durations in a linyphiid. When the beginning of copulation is set at time 0, the times to completion of the first copulation fall along a straight line ( $r^2 = 0.98$ ; Fig. 5). This suggests that the copulations were nearly uniformly distributed. However, the second copulation was better described by a negative logarithmic ( $r^2 = 0.95$ ) than a linear function ( $r^2 = 0.85$ ). While measures of latency (in this case duration of copulation) are often positively skewed, first copulations (skew = 0.27; normality = 0) were less positively skewed than second copulations (skew = 0.97).

*Prolonged second copulation:* Males ( $n = 15$ ) that had mated on only one side of a newly-molted female were presented to a second newly-molted virgin female. All males employed the unused palp. They followed the same pattern of copulatory durations as a male mating on both sides of a single female. There

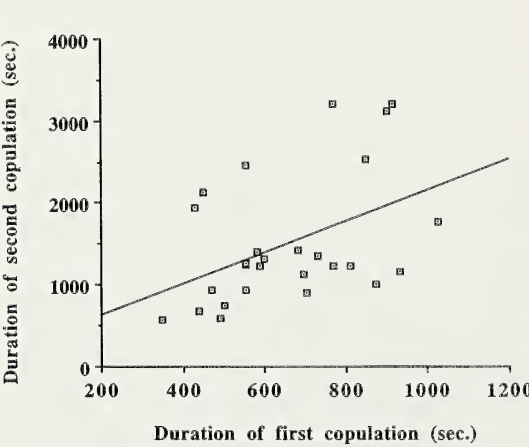


Figure 4.—Relationship between the durations of the first and second copulations. Males ( $n = 27$ ) that copulated longer for the first copulation also copulated longer during the second copulation ( $r = +0.44$ ;  $Y = 248.8 + 1.91X$ ).

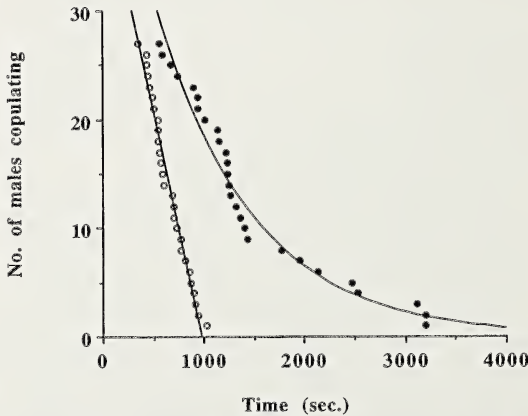


Figure 5.—When the start of copulation is set at time 0, the number of males remaining *in copula* over time for the first copulation (○) is best described by a linear function ( $Y = 42.4 - 0.004X$ ) and for the second copulation (●), a negative exponential function ( $Y = 53.146 (10^{-0.0005}X)$ ).



was no significant overall difference in the copulatory durations of males given one or two females ( $F_{1,28} = 0.29$ ,  $P = 0.60$ ). Overall, second copulations were significantly longer than first copulations ( $F_{1,28} = 26.28$ ,  $P < 0.0001$ ). However, the durations of the first and second copulations did not differ as a function of the number of females with which the males mated ( $F_{1,28} = 0.75$ ,  $P = 0.39$ ). For all males that mated with two females, first copulations ( $572 \pm 147$  sec) were much shorter than second copulations ( $1721 \pm 814$  sec).

**Post-copulatory sperm induction.**—After a male mated twice with a virgin female, it remained near, and rarely on, the female's web for a short time, grooming palps, legs and gonopore. The male moved 1–3 m from the female's web and resumed grooming until sperm web construction was initiated,  $47.5 \pm 16.9$  min ( $n = 15$ ) after the final dismount. We do not know if males that mated only once with a female induct sperm prior to another mating.

The sperm web was constructed on a single horizontal strand 5–60 cm in length. After making several passes along this line, the male laid another strand, 3–4 cm in length, basically parallel to and near the middle of the first. The two strands were held apart by legs I and II and legs III and IV. The latter pairs were extended and held out in front of the body so that an elongated, horizontal hexagon was formed. Silk was then laid in a zigzag manner between the two lateral sides of the hexagon. The area proximal to the cephalothorax was completely covered with silk, and it was to the ventral side of this area (approximately  $1.0 \times 1.5$  mm) that the male applied the gonopore. After many (about 100) applications, the male tipped its body up so it was perpendicular to the plane of the sperm web. He then reached over the dorsal side of the sperm web and applied the palps. It should be noted that one male (not included in this data set) had a broken fourth femur and could not keep the sperm web from collapsing before induction even though it constructed five webs.

Palps were individually dipped a mean of  $4.6 \pm 1.9$  times before they were switched. Dips were extremely shallow, a travel distance of less than 1 mm. Observation of this behavior was difficult and made worse by the slightest breeze. Males ( $n = 15$ ) exhibited  $7.4$

$\pm 1.9$  and  $7.9 \pm 1.8$  induction bouts for the right and left palp, respectively. Sperm induction took  $5.3 \pm 2.0$  min ( $n = 15$ ) to complete. The male then moved off the sperm web, which immediately collapsed, and departed. Observations were made only until the first sperm induction was completed, so males could have built additional sperm webs later.

**Oviposition.**—Females oviposited between July and October with most clutches laid in August and September. Of 101 marked adult females in 1990, 57 survived and remained in the study area to lay at least one clutch. Of the others, 13 were seen only the day they were marked and 31 disappeared before oviposition, after an average of  $17.8 \pm 9.6$  days. Females ( $n = 8$ ) that were observed molting, mating and ovipositing laid their first clutch an average of  $30.7 \pm 8.2$  days after the molt.

Most oviposition occurred within 5 m of the web site and within 1–3 m of the ground ( $2.5 \pm 0.88$  m,  $n = 97$ ). Most egg sacs (66%,  $n = 63$ ) were found in boxelder (*Acer negundo*), one of the more common trees in the area. The eggs were laid near the center of the underside of a leaf that was folded transversally and sealed tightly. The resulting sac was triangular in appearance with silk threads connecting the egg sac to the intersection of the leaf petiole and connecting branch. We have not observed *M. gracilis* constructing egg sacs but females left the web site sometime after dusk, and the procedure was usually completed by 0900 h the following morning. By this time most females had returned to their previous web site.

Females that had oviposited at least once ( $n = 57$ ) produced  $1.6 \pm 0.8$  clutches before they died or disappeared. Examination of five clutches laid during the middle of the egg-laying season revealed  $266.8 \pm 11.5$  eggs. Clutches weighed  $67.1 \pm 4.2$  mg, and individual eggs  $0.25 \pm 0.02$  mg. The eggs were ovoid,  $0.80 \pm 0.03$  mm ( $n = 50$ ) in length and  $0.66 \pm 0.02$  mm in width. By multiplying the mean number of egg clutches (1.6) by the mean number of eggs per clutch (266.8), the average female might lay 425 eggs throughout her lifetime.

*M. gracilis* egg sacs appeared to us to be cryptic, yet most suffered predation. Of 75 egg sacs found in the egg sac census areas (sacs laid by unmarked females), 62 (83%) were already destroyed at initial examination. Intact egg sacs ( $n = 13$ ) lasted for a mean of



only 3.9 days before we found that they had been opened and contents removed. Another 22 clutches laid by individually-marked census females (the female was found on the egg sac) did not fare much better. Overall, these lasted a mean of 10 days, however, many (41%;  $n = 10$ ) were eaten within 48 h of being laid. Four egg sacs lasted between 18–57 days before either being eaten or falling to the ground. Only two egg sacs were intact as of mid-October. They hatched 37 and 41 days, respectively, after being laid. Within two weeks of hatching the spiderlings had molted.

When there was evidence of predation, the entire egg mass had usually been pulled from the sac. The white silk that normally surrounded the eggs was outside the sac, in an elongated cotton-like mass. Except for egg sacs that fell to the ground ( $n = 3$ ), they all ( $n = 94$ ) appeared to have been destroyed by a similar means of attack.

## DISCUSSION

In many spider species, males mature in fewer molts than females. Consequently, males mature before females and are often smaller (Vollrath & Parker 1992). We found that these sex differences apply to *M. gracilis*. Sexual bimaturation is thought to be related to male sperm priority patterns (Parker 1984; but see Head 1995). When the first male to mate with a given female fertilizes most of her eggs, selection should favor males that mature early in the season so they are present when the female molts to adulthood and becomes sexually receptive (Austad 1984). Male advantage pattern for fertilizing a female's eggs has been determined for six entelegyne spiders, those with a heavily sclerotized female reproductive tract and separate sperm uptake and fertilization ducts. Most show basically a first male advantage (Jackson 1980; Vollrath 1980; Austad 1982; Martyniuk & Jaenike 1982; Christenson & Cohn 1988; Watson 1991; Masumoto 1993; but see Andrade 1996). Given that *Micrathena* is an entelegyne and shows early male maturation, we suspect it, too, will show a first male advantage pattern for fertilizing a female's eggs.

Male *M. gracilis* are found more frequently on the webs of penultimate-instar females, particularly those approaching the final molt. Jackson (1986), Watson (1990), Dodson & Beck (1993) and others (cited in Christenson

1984) have noted cohabitation with females just prior to their final molt and initial sexual receptivity. If *M. gracilis* does show a first male advantage pattern for fertilizing a female's eggs, the tendency of males to remain with penultimate-instar females is understandable as the female mates for the first time just after her final molt. We suspect that male *M. gracilis* can monitor an impending molt. As has been noted by Dodson & Beck (1993), the monitoring of the female must be frequent or continuous so that the male does not miss the female's molt and lose her to another male. We don't know how a male recognizes such a female, but there are at least four possibilities. First, females do not build a viscid spiral within a few days prior to the final molt, so a changing vibratory environment could cue the male. This would not, however, help the male determine when molting has occurred because the viscid spiral is not constructed three days prior to the final molt. Second, *M. gracilis* have stridulatory organs (Hinton & Wilson 1970; Uetz & Stratton 1982) that could be used to signal an approaching molt. Such communication may be relatively cryptic to the human observer and we may have missed it. Third, Hill & Christenson (1988) note that smaller juvenile *Nephila clavipes* (Linne 1767) females are more aggressive toward the male than are penultimate-instar females, so males may be responding to female aggressiveness. We did not note such a change in aggressiveness in *M. gracilis* females. Fourth, the female could produce a male-attracting pheromone. Female spiders are known to produce pheromones (Olive 1982; Watson 1986; Prenter et al. 1994) that have only recently been isolated and identified (Schulz & Toft 1993).

Male *M. gracilis* are unable exclude other males from approaching the female. At best, a male might interfere with another's courtship activities. It is worth noting that a male on a female's web is cohabiting and not actually defending or guarding the female. We think that there are two major reasons that guarding may not have evolved. First, guarding may not occur because it is impossible to guard the female and her web effectively. The viscid spiral of the female *M. gracilis* web is not held in place by a complex of barrier strands and is essentially two-dimensional. Thus, there is no central location near the fe-



male a male could occupy and prevent access by other males. This hypothesis is further supported by that observation that a male must attract a female to his location to mate via the mating thread. Competing males could entice the female to mate from any point along the perimeter of the viscid spiral. A male on one side of the viscid spiral is unable to prevent another male from accessing the female on the opposite side of the viscid spiral. In contrast, some orb-weavers, such as *Nephila clavipes*, construct an enduring three dimensional orb-web, one containing the viscid spiral held in place by many barrier or support strands. Many of the barrier strands connect near the hub opposite the female and a male can remain there, centrally located, and fend off other males as they approach from virtually any direction (Christenson & Goist 1979). Copulation occurs just after the final molt at the hub. Therefore, a male occupying the hub position almost always mates while males at the periphery of the web rarely ever mate with that female (Christenson & Goist 1979). Further evidence of a lack of functional guarding is that the male cannot fend off rival males while copulating and he must dismount the female after the first copulation. The female responds to courting males, even when *in copula*, so if courting is occurring during a dismount, the female can mate with another male.

A second major reason that guarding may not have evolved is that guarding one mate might be less profitable than searching for and mating with other females and thus it has not been selected for in males. The interval between mating just after the final molt and oviposition is about one month. This is a relatively long period of time for a male to remain and defend a sexually active female against other male visitors. If there is a strong first male advantage pattern for fertilizing a female's eggs, then little might be gained from guarding a mate given that subsequent males will fertilize very few of the female's eggs. In addition, the male's investment with a particular female might well be lost due to predatory pressure on egg sacs. Our data indicate that female *M. gracilis* lay one or two egg sacs that are likely not to produce spiderlings in the spring. Loss of investment through spiderling mortality is a relatively understudied phenomenon. We agree with Pitnick & Mar-

kow (1994) that in species where the female produces relatively few egg sacs that suffer relatively high mortality, a male would benefit from mating with as many females as possible rather than guard a single female. This would increase the likelihood that he would sire or contribute to a surviving clutch.

Like many spiders, a *M. gracilis* male must mount the female twice to inseminate both of the female's pores. Proximally, males must dismount the female between copulations because of the relatively complicated process of genitalic coupling. Male spiders must often assume very specific orientations to the female in order to insert the palp (Foelix 1980). The evolution of male genitalia is thought to be influenced by sexual selection on females (Eberhard 1985). Ultimately, females might influence the evolution of male specific insertion orientations and structures that prevent the male from inserting both palps in a single mounting. Coyle & O'Sheilds (1990) have suggested that female spiders might have evolved multiple spermathecae to prevent a male from monopolizing access to all of her sperm storage sites. We agree and suggest that female spiders might also have evolved specific insertion orientation requirements to prevent a male from monopolizing both tracts in a single mounting. Such an arrangement might allow a female to gain information about the quality of a male during the first copulation and between the first and second copulation. She could then allow or refuse the male access to the opposite tract based on that information.

A precondition for the kind of asymmetry in copulatory duration that we document here is a male mating once on each side of the female. Insertions separated by a dismount and preceded by overt courtship appears to be the rule in the spiny orbweavers (sub-family Gasteracanthinae; Robinson & Robinson 1980) and other Araneidae (Bristowe 1929; Robinson & Robinson 1980). What aspects of araneid natural history would drive the evolution of copulations consisting of one insertion on each side of the female? Our descriptive work indicates that general aspects of *M. gracilis* reproduction are fairly typical for the family, that is, females are solitary, sedentary predators while males move from female to female. Males do not remain and defend mates, they often copulate with several females, and females mate with more than one



male. We suspect that their pattern of mating behavior, two copulations separated by a dismount with the second copulation being much longer than the first, is influenced by the ease with which a second male can copulate with the female within a relatively brief period of time.

Under certain circumstances selection should favor males that rapidly transfer sperm to one reproductive tract in a single insertion (copulation) rather than over a series of insertions. If a male is required to dismount in order to re-insert in the same epigynal opening, a second male could usurp the first male on that side. Our observations suggest that the likelihood of such usurpations is related to particular elements of reproductive natural history: males mature before females and many males may simultaneously cohabit with a single female, a web structure that does not allow a male to defend the female from competitors, and the use of a mating thread to entice the female to mate. There is no central area on the web near the female that the male can occupy, consequently a male must entice the female to his location in order to insert.

Male *M. gracilis* appear highly motivated to copulate with both tracts of the virgin female. If the suspected first male advantage pattern in fertilization is related to the conduit shape of the spermathecae, then the sperm priority pattern would be determined separately for each tract. The advantage would not go to the first male to mate with a female, *per se*, but to the first male to mate with a given tract. Therefore, a male should attempt to copulate on both sides. A male that copulates only once would leave the other virgin tract available for insemination by other males. Unless females can preferentially use sperm from one tract over the other at oviposition, the first male is likely to cede 50% or more of the fertilizations to a second male that mates with the remaining virgin tract.

The failure to obtain two copulations with a given female is likely to have important implications for the male's subsequent reproductive activities. About 25% of the males failed to copulate twice with a given female. These males would leave the females with one palp filled with sperm and one empty palp. A male in this circumstance might either refill the empty palp or mate with the next female using one full and one empty palp. It is unclear

whether two copulations are required to trigger the onset of sperm induction and whether a male could preferentially fill the empty palp. Given the rhythmic and stereotyped organization of sperm induction behaviors, it is unlikely that a male could preferentially fill one palp. The filling of the empty palp may, in turn, influence whether a male copulates once or twice with the next female.

The distributions of the durations of first and second copulations suggest that different selective forces might be operating. The durations of the first copulations were short and nearly normally distributed which suggests that stabilizing selection is operating. The durations of the second copulation were longer and more positively skewed, suggesting directional selection on longer copulatory durations. Given that a male cannot exclude the advances of other males, selection should operate on speed and efficiency of sperm transfer during the first copulation so that he can switch sides before another male moves onto the web. That directional selection is operating on longer second copulations suggests that the second copulation may serve somewhat different functions than the first. All phases of the second copulation were prolonged. We have shown that the prolonged copulation can facilitate sperm storage on both sides of the female and may serve a mate guarding function as well (Bukowski & Christenson 1997, unpubl. data). Such differences in copulatory durations have been reported in other species of a number of spider families (Bristowe 1929; Huber 1993, 1995; Sasaki & Iwahashi 1995) and similar functions might be served.

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## MATING BEHAVIOR OF *PHYSOLIMNESIA AUSTRALIS* (ACARI, LIMNESIIDAE), A NON-PARASITIC, ROTIFER-EATING WATER MITE FROM AUSTRALIA

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**ABSTRACT.** The diversity of sperm transfer behavior shown by water mites (Acari, Hydrachnidia) is among the highest in the Arthropoda. However, sperm transfer has been described in fewer than 10% of water mite genera, all of them being Holarctic or cosmopolitan taxa. Here I describe mating behavior in *Physolimnesia australis* (Halik 1940), the sole representative of an Australian genus. *P. australis* is unusual in having larvae that do not parasitize insects, and in including rotifers in its diet. The highly dimorphic *P. australis* male responds to female presence by taking up an “embrace” posture in which he orients his opisthosoma and legs III toward approaching females. The female is caught in the embrace and her legs IV are secured by the modified tips of the male's legs IV. The male deposits a glutinous mass on the female's back, which she grooms towards her genital opening after being released. This mode of transfer differs from members of the confamilial genus *Limnesia* Koch 1836 in which males and females do not pair.

Chelicerates show the greatest diversity of sperm transfer modes in the Arthropoda. In some taxa, males transfer sperm directly with a penis (Opiliones) or with secondarily derived genitalia (e.g., palps in Araneae). In other groups, males transfer sperm indirectly by depositing spermatophores on a substrate, and either encouraging females to move over the sperm packets (e.g., Scorpionida) or allowing females to discover and take up sperm on their own (e.g., many Pseudoscorpionida) (Proctor et al. 1995). Finally, the horseshoe crabs (Merostomata) have external fertilization of eggs (Ruppert & Barnes 1994). Within the Chelicerata, some taxa exhibit greater behavioral diversity than others. For example, all spiders pair whereas pseudoscorpions may or may not have close associations between the sexes. The greatest variety of sperm transfer behavior occurs among the mites (Subclass Acari), and within this group the most diverse behavior is shown by the water mites (Suborder Prostigmata, Hydrachnidia). With the exception of external fertilization, all possible modes of sperm transfer occur in the Hydrachnidia from direct transfer via venter-to-

venter copulation (e.g., *Midea* Bruzelius 1854, *Eylais* Latreille 1796) to complete dissociation in which the sexes never meet (e.g., *Hydrodroma* Koch 1837). Despite this amazing range of behavior, water mites have been poorly studied and mating observations have been published for only 24 of the more than 340 genera of water mites (Proctor 1992a,b). These observations have been limited almost entirely to species from North America and Europe, and there are no descriptions of sperm transfer in a non-holarctic genus. Here I describe mating behavior in a monotypic genus of Australian water mites together with casual observations of its life cycle and diet.

### METHODS

*Physolimnesia australis* (Limnesiidae) is a small ( $\leq 1$  mm) water mite found in the littoral zone of standing and slowly running water in Queensland and New South Wales (M. Harvey pers. comm.; Proctor pers. obs.). This species shows a strong sexual dimorphism in which males have a ventrally concave opisthosoma and flattened terminal segments of legs III and IV (Fig. 1). Females are morphologically similar to species in the confamilial genus *Limnesia* and were previously described

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as a species in this genus (*Limnesia trituberculata* Viets 1955). I collected and observed *P. australis* on two occasions in 1995: in March from Cedar Creek approximately 50 km south of Brisbane, Queensland; and in October from a large pond on the University of Queensland campus, St. Lucia. All observations were made using a dissecting microscope and took place at the Department of Entomology, University of Queensland. I separated mites according to sex and stage (adult and deutonymph) and maintained these groups in large well plates (well diameter = 35 mm, depth = 19 mm). Dipteran larvae (Culicidae, Chironomidae) and cladocerans (Moinidae) collected from a small pond on the University of Queensland campus were included as potential prey for the mites. I made behavioral observations on mites that had been collected as adults as well as those raised from deutonymphs in the lab. Voucher specimens are deposited in the University of Queensland Insect Collection, Department of Entomology, St. Lucia, Australia, 4072.

## RESULTS

**Life-cycle and predation.**—Most water mites have a complex life-cycle with three active stages: the six-legged larva parasitizes adult aquatic insects, and is followed by two eight-legged predatory stages, the deutonymph and the adult (Smith & Cook 1991). *Physolimnesia australis* is an exception to this rule in that its larvae forgo the parasitic phase. Adult females collected from the field readily laid small clutches consisting of 1–8 eggs on the sides and bottoms of the wells. The eggs were large relative to the female (mean = 134  $\mu$ m, SD = 8  $\mu$ m,  $n$  = 4). I observed that *P. australis* larvae remain within the coating of the egg clutch and transform directly into predaceous deutonymphs (via the inactive protonymph).

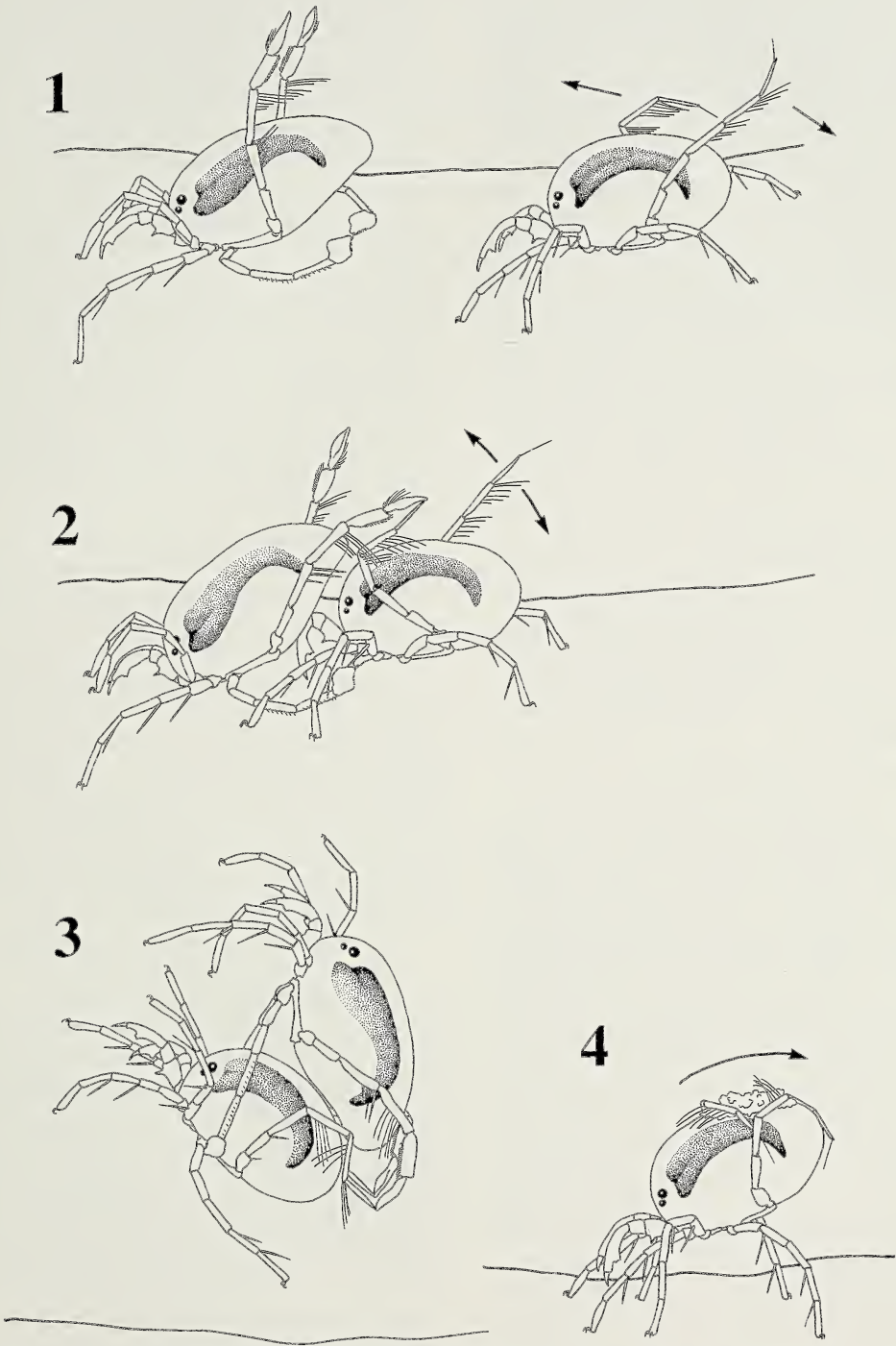
The newly emerged *Physolimnesia* deutonymphs were very small (body length  $\approx$  250  $\mu$ m) and were unable to handle the large cladoceran and dipteran prey I provided. Nevertheless, they increased in size and transformed into adult mites. This energetic mystery was solved when I observed deutonymphs capturing and eating large phoretic rotifers that had been inadvertently introduced along with their moinid cladoceran hosts. The rotifers were identified as *Brachionus variabilis* Hempel

1896, a cosmopolitan epizootic species of 200–380  $\mu$ m in length (Koste & Shiel 1987). Thus to a 250  $\mu$ m deutonymph, a single rotifer would be a substantial meal. Adult male and female *P. australis* were observed eating *B. variabilis*, as well as feeding on cladocerans and dipteran larvae. Neither the deutonymphs nor the adults appeared to forcibly remove the rotifers from their moinid hosts; rather, the mites captured rotifers that had detached from the cladocerans and were swimming freely in the wells.

**Mating behavior.**—When a male *P. australis* was placed in a well that held females, he initially stood on the substrate and groomed himself vigorously by moving legs III and IV back over his dorsum and around to his venter. After a bout of grooming, the male was very still relative to the females, which were constantly crawling and swimming close to the substrate. In *P. australis*, as in most limnesiids (pers. obs.), crawling locomotion is accomplished by the first three pairs of legs, with legs IV moving in a constant fanning motion over the mite's back, presumably aerating the dorsal integument for gas exchange purposes. When a female bumped into the male or passed near him he immediately took up the "embrace" posture (Fig. 1). In this position the male's opisthosoma was tilted at approximately 30° to the substrate, the flattened tips of legs III were touching and pressed against the substrate (thereby forming the circular "embrace"), and legs IV were held rigidly and vertically. The male oriented his embrace towards any females that passed behind him. He also oriented towards other passing males and occasionally to swimming cladocerans. While in this posture the male was often approached by a female that -by accident or intent -crawled up behind the male and placed her capitulum over the flattened tips of the male's legs III (Fig. 2). The male responded by elevating his opisthosoma to about 50° to the substrate and attempting to capture the fanning tips of the female's legs IV in the flattened, scoop-like tips of his own fourth legs (Fig. 2). It was unclear how this capturing was achieved; possibly, the long apical seta at the tip of the female's leg IV is secured by the groove in the male's tarsus.

When the male had captured both of the female's legs she typically began to struggle.





Figures 1-4.—Mating behavior of *Physolimnesia australis*. 1, Male in the "embrace" posture with female approaching from behind; 2, Female within male's embrace, male has captured the tip of her left leg IV in the tip of his modified leg IV; 3, Male has captured both leg tips and the pair is swimming jerkily; 4, Female grooms sticky material deposited by male on her back towards her ventrally located genital aperture.

However, the male gripped the female in the region of her 2nd or 3rd coxal plates with the tips of his legs III (Fig. 3). The pair typically left the substrate at this point and swam about in a jerky fashion. I observed at least 20 pairings that reached this stage; however, all but three were terminated when the female escaped from the male's grip after a few seconds of swimming. For the pairs that continued swimming, which usually lasted less than one minute, the male rubbed the concave ventral surface of his opisthosoma on the female's dorsum. The male's genital opening is located just behind the coxal plates of legs IV, and the rubbing of his venter against the female's back probably represents deposition of the ejaculate. In two of the three complete matings observed, the male slid around backwards towards the end of the female's opisthosoma just before the pair separated. After the female escaped or was released from the male's grip, she perched on the substrate and vigorously groomed back over her dorsum and around towards her ventrally located genital opening (Fig. 4). In two of the three complete matings, I observed opaque white material on the female's dorsum after she separated from the male (Fig. 4).

## DISCUSSION

The mating behavior of *Physolimnesia australis* is very different from that of species in the genus *Limnesia*, the only other limnesiid genus for which reproductive behavior is known. *Limnesia* species show no sexual dimorphism save in body size (female larger) and degree of fusion of genital plates. In *Limnesia* spp., physical or chemical contact between males and females is not required for spermatophore production and transfer (Witte 1991; Proctor 1992a). Rather, males maintained alone will deposit spermatophores on a substrate, and females that later encounter them will take up sperm if so inclined. Proctor (1992a) called this mode of sperm transfer "complete dissociation", and contrasted it with three other modes: incomplete dissociation (physical or chemical contact between the sexes required for spermatophore deposition but no pairing between the sexes); pairing, indirect transfer (male courts a given female, spermatophores deposited on substrate); and copulation (male places sperm in female's sperm-receiving structure). The transfer mode

of *Physolimnesia australis* appears to fall between the third and fourth categories, as the male places the sperm on the female (as in copulation), but she must move it to her genital opening (as in pairing, indirect transfer). This suggests that the categories of sperm transfer outlined by Proctor (1992a) may be too rigid to easily encompass all transfer behaviors.

It is not clear what motivates the *P. australis* female to enter the embrace of the male's legs. In the water mite *Neumania papillator* (Unionicolidae), the female orients towards the male's courtship signals because they resemble vibrations caused by prey (Proctor 1991). It is possible that male *Physolimnesia australis* engage in similar "sensory trapping" (*sensu* Christy 1995), perhaps by producing chemicals that mimic the scent of prey animals.

The water mite Family Limnesiidae contains 23 genera, five of which are composed of species that are strongly sexually dimorphic (*Physolimnesia*, *Timmsilimnesia* K.O. Viets 1984, *Centrolimnesia* Lundblad 1935, *Pterolimnesia* Viets 1942 and *Acantholimnesia* Viets 1954) (Cook 1974, 1980, 1986, 1988; Viets 1984). No two genera share the same types of male modifications, suggesting that sperm transfer with close contact between the sexes has evolved repeatedly in this family from an ancestral non-paired state, as has occurred in many other families of water mites (Proctor 1991).

*Physolimnesia australis* is an unusual water mite in other aspects of its biology. Whereas most Hydrachnidia have a parasitic larva that acts as both a feeding and a dispersal stage, the larva of *P. australis* transforms to a predatory deutonymph without parasitizing an insect host. Suppression of the parasitic phase has been recorded in 29 species scattered through distantly related families of water mites, including a few confamilials in the genus *Limnesia* (Smith & Cook 1991; Smith in press; H. Proctor pers. obs.). Like many species with non-feeding larvae, *P. australis* has a small adult body size, small clutch size and relatively large eggs for its body size (Cook, Smith & Brooks 1989; Smith in press). Although the loss of larval parasitism has independently arisen many times, it does not seem conducive to cladogenesis, as such lineages consist of single species (or populations)



whose closest relatives retain parasitic larvae (Smith in press). Although one might expect that loss of dispersal via parasitic larvae would occur in lineages that inhabited permanent water bodies, there is no apparent pattern in relation to habitat: lineages without larval parasitism occur in streams, temporary ponds, and both littoral and planktonic habitats within lakes (Smith in press). It is not clear how, or indeed if, water mites with non-feeding larvae disperse to new bodies of water.

The final strange aspect of *P. australis*' biology is the inclusion of rotifers in its diet. Confamilials in the genus *Limnesia* have been observed feeding on a variety of invertebrates (crustaceans, insects, other mites) and even vertebrate prey (fish eggs) (Proctor & Pritchard 1989); but to my knowledge, this is only the second observation of arachnids feeding on rotifers. One other species, an undescribed oribatid mite in the genus *Aquanothrus* Engelbrecht 1975 (Ameronothridae), is believed to feed on rotifers based on the presence of undigested trophi (rotifer mouthparts) in the mites' guts (R.A. Norton pers. comm.).

*Note added in proof:* (a) Adults and nymphs also prey on nematodes and oligochaetes. (b) It is also possible that the male deposits spermatophores on his own legs III prior to taking up the embrace posture; sperm could thereby be inserted in the female's genital opening during the "nuptial swim," and the gelatinous substance on her dorsum may be residual spermatophore material.

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## ON THE ABUNDANCE AND PHENOLOGY OF PALPIGRADI (ARACHNIDA) FROM CENTRAL AMAZONIAN UPLAND FORESTS

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**ABSTRACT.** The 745 paligrads (micro-whip scorpions) collected in a 12 month period in the soil (0–7 cm depth) of a secondary upland forest ( $120.1 \pm 50.8$  ind./m<sup>2</sup>/month) and of a primary upland forest ( $29.4 \pm 20.2$  ind./m<sup>2</sup>/month) near Manaus all belong to the species *Eukoenia janetscheki* Condé 1993. About 75% of all specimens inhabited the mineral subsoil (3.5–7 cm depth) where monthly catches were negatively correlated with temperature and moisture content of the soil. Females were almost twice as abundant as males. The lack of a distinct reproductive period and the presence of juveniles and adults (both sexes) throughout the year indicate a plurivoltine mode of life. No specimens were caught on or above the soil surface. Abundances of *E. janetscheki* are compared with those of the Schizomida (tatarids) and Thelyphonida (vinegaroons) from the same study sites. *E. janetscheki* also represented the paligrads obtained from the soil of three other upland forest types in Central Amazonia (0–14 cm depth) and accounted for 0.1–0.3% of the total arthropod fauna.

Terrestrial arthropods of Central Amazonian forests have been investigated for several years (Adis & Schubart 1984; Adis 1997; Adis et al. 1997b,c) cooperatively between the National Institute for Amazonian Research (INPA) at Manaus/Brazil and the Tropical Ecology Working Group at the Max-Planck-Institute for Limnology in Plön/Germany (Projeto INPA/Max-Planck). Data on abundance and phenology of Paligradi sampled during a 12 month period in 1982/83 in both a primary and a secondary upland forest are now available, as their time-consuming taxonomical evaluation has been completed (Condé 1993, 1997). Our data represent the very first contribution on the phenology of a tropical paligrad species: *E. janetscheki* Condé 1993. Voucher specimens have been deposited at the Systematic Entomology Collections of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Brazil, at the Muséum d'histoire naturelle in Genève, Switzerland and at The Field Museum, Chicago, USA.

Results presented are compared with abundance data of *E. janetscheki* from three other upland forest types near Manaus, and which were sampled between 1985 and 1991.

### STUDY AREA AND METHODS

Paligrads were collected between 1981 and 1983 in the course of ecological studies on Central Amazonian arthropods from two previously investigated and fully described forest types, all within 30 km of Manaus: (1) primary upland forest at Reserva Florestal A. Ducke (= Reserva Ducke; 2°55'S, 59°59'W) on the Manaus-Itacoatiara highway (AM-010 at km 26; cf. Penny & Arias 1982), (2) secondary upland forest at Rio Tarumã Mirim (3°2'S, 60°17'W), a tributary of the Rio Negro, where the vegetation was previously cut but unburned (Adis 1992). Both forests are subject to a rainy season (December-May: average precipitation 1550 mm) and a "dry" season (June-November: average precipitation 550 mm, but each month has some rain events; cf. Ribeiro & Adis 1984). The yellow



latosol of the primary and secondary upland forests supported a 2–3 cm thick humus layer, interspersed with fine roots, and a thin surface covering of leaf-litter. One ground photo-elector (emergence trap) and one arboreal photo-elector for trunk ascents (funnel trap) were installed in both forests from December 1981 to December 1982 (Adis & Schubart 1984). Distribution of palpigrads in the soil was studied between September 1982 and August 1983 (Morais 1985; Rodrigues 1986). Twelve soil samples were taken once a month from each forest type at random along a transect with a split corer (= steel cylinder with lateral hinges; diameter 21 cm, length 33 cm) which was driven into the soil by a mallet. The combined area of 12 samples represented 0.42 m<sup>2</sup>. Each sample of 7 cm depth was then divided into two subsamples of 3.5 cm each. Animals were extracted from subsamples following a modified method of Kempson (Adis 1987). The monthly collection data of palpigrads from the two soil layers in relation to changing conditions of precipitation, temperature and humidity of the air near the forest floor as well as moisture content, temperature and pH of the soil were statistically evaluated with a linear correlation test (Cavalli-Sforza 1972) using the original field data (cf. Morais 1985; Rodrigues 1986) of the previous month. In addition, the presence of palpigrads in tree crowns of the primary upland forest was tested by fogging canopies with pyrethrum (with and without synergist) during the dry and rainy seasons (July 1977, August 1991, February & August 1992, July 1994; Adis et al. 1984, 1997a). Palpigradi sampled were classified as juveniles, subadults and adults (males and females) according to Condé (1984a,b, 1993, 1997).

## RESULTS

Palpigradi obtained from different upland forest types in the vicinity of Manaus were represented by only one species: *Eukoenenia janetscheki* Condé 1993. The body length of adult males (without flagellum) reached 1 mm.

A total of 146 specimens was collected in the primary upland forest at Reserva Ducke and 599 specimens in the secondary upland forest at Rio Tarumã Mirim. Out of these, 92% could be identified to their developmental stages. *E. janetscheki* was only found in

the soil and never caught on tree trunks or in the canopy. No specimens were captured in ground photo-electors. In the primary upland forest, palpigrads represented 0.2% and in the secondary upland forest 0.6% of the total arthropods extracted from soil samples within 12 months (Acari and Collembola omitted; cf. Morais 1985; Rodrigues 1986). Their abundance in 0–7 cm soil depth was comparable to that of the Schizomida (Fig. 1). Most specimens of *E. janetscheki* inhabited the mineral subsoil (Fig. 2: 3.5–7 cm) and a few (22–26%) the organic layer (0–3.5 cm depth). An average of  $120.1 \pm 50.8$  ind./m<sup>2</sup>/month was recorded in the secondary upland forest and  $29.4 \pm 20.2$  ind./m<sup>2</sup>/month in the primary upland forest (0–7 cm depth). More than 50% of the total catch in both forests was represented by adults (Fig. 2). Sex ratio (adult males to females) in the secondary forest was 1:1.8 (81% of the total adults could be sexed).

In the secondary upland forest, the monthly abundance of *E. janetscheki* in the mineral subsoil (3.5–7 cm depth) was negatively correlated with soil temperature, i.e., catch numbers (in particular of subadults) decreased with increasing temperatures (total catch:  $r = -0.7454$ ,  $P < 0.01$ ; adults:  $r = -0.5926$ ,  $P < 0.05$ ; subadults:  $r = -0.8614$ ,  $P < 0.001$ ;  $n = 12$ , respectively). In the primary upland forest our data indicated a negative correlation of adults with the soil moisture content in the mineral subsoil ( $r = -0.5670$ ,  $P < 0.1$ ,  $n = 12$ ). The total catches of specimens obtained during the dry season and the rainy season were similar: 66% versus 34% in the primary upland forest and 61% versus 39% in the secondary upland forest, respectively. However, there was no distinct reproductive period in the secondary forest (where *E. janetscheki* was more abundant) because juveniles as well as adults (both sexes) occurred throughout the year (Fig. 3). These results indicate a plurivoltine mode of life.

## DISCUSSION

Comparable data on the abundance and vertical distribution of the soil fauna in three different upland forest types of Central Amazonia were given by Adis and collaborators (Adis et al. 1987a,b; 1989a,b; Ribeiro 1994). Arthropods were collected to a soil depth of 14 cm during rainy and dry seasons and extracted with the Kempson method as de-

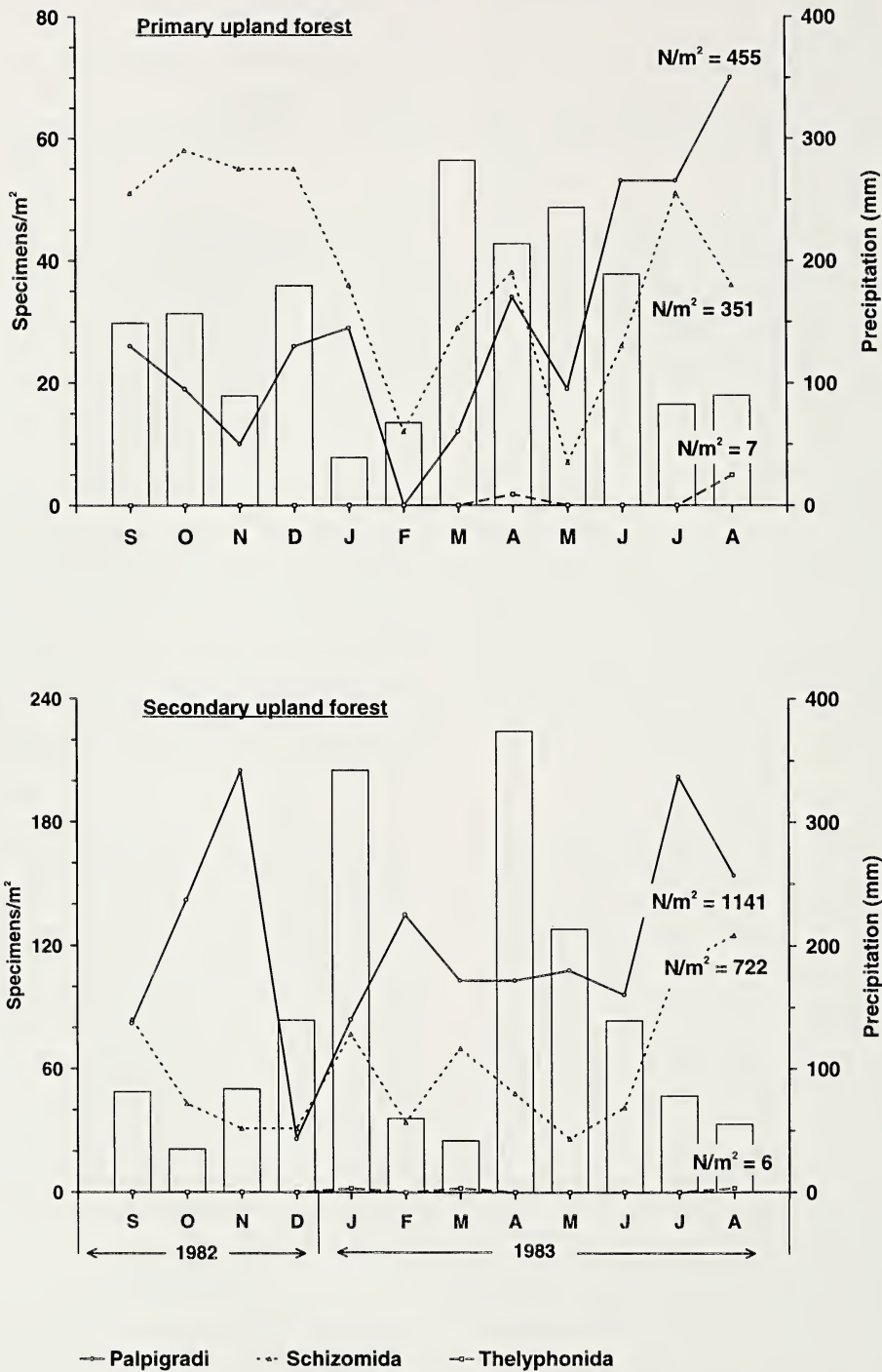


Figure 1.—Distribution of Palpigradi, Schizomida and Thelyphonida in the soil. Samples taken monthly at 0–7 cm depth between September 1982 and August 1983 in two upland forests near Manaus. (Total catch = 100% in each forest type;  $n$  = total number of specimens). Total precipitation per month given between sampling dates (= at the end of each month in the primary upland forest and in the middle of each month in the secondary upland forest). The low rainfall observed in early 1983 was due to a strong El Niño event (see Adis & Latif 1996).



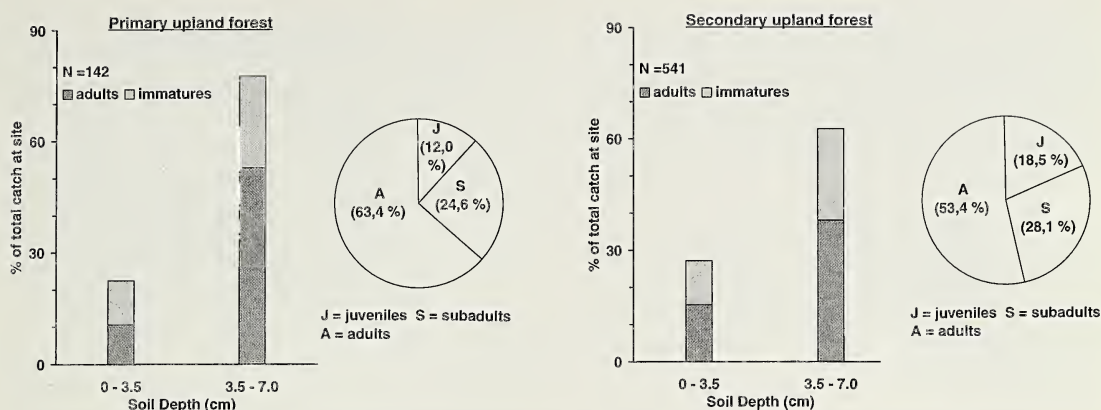


Figure 2.—Distribution of *Eukeonenia janetscheki* in the soil according to soil depth, and percentage of all developmental stages in two upland forests near Manaus. (Total catch = 100% in each forest type). Samples taken monthly at 0–3.5 and 3.5–7 cm depths between September 1982 and August 1983.  $n$  = total number of specimens.

scribed above. Between 75% and 92% of all arthropods were found to inhabit the top 7 cm when Acari and Collembola were included in the total catch numbers and 69%–84% when they were omitted. Data on Palpigradi (= *E. janetscheki*; see Condé 1997) are now available.

One study was conducted in 1985/86 in a secondary upland forest on yellow latosol at the INPA campus in Manaus, where the vegetation was previously cut but unburned (Adis et al. 1987a,b). Palpigrads represented 0.2–0.3% of the total arthropods when Acari and Collembola are included (dry season: 50.448 ind./m<sup>2</sup>, rainy season: 63.850 ind./m<sup>2</sup>) and 0.9% when they are omitted from the total catch numbers (dry season: 11.934 ind./m<sup>2</sup>, rainy season: 17.886 ind./m<sup>2</sup>). In the mineral subsoil (7–14 cm depth), the abundance of palpigrads was higher during the dry season (62% of the total catch; 62.6 ind./m<sup>2</sup>) but lower during the rainy season (44% of the total catch; 72.2 ind./m<sup>2</sup>) when compared to the top 7 cm.

Another study was made in 1990/91 in a secondary upland forest on yellow latosol, about 50 km north of Manaus, where the vegetation was previously cut and burned (Ribeiro 1994). Palpigrads represented 0.1–0.2% of the total arthropods when Acari and Collembola are included (dry season: 33.915 ind./m<sup>2</sup>, rainy season: 19.696 ind./m<sup>2</sup>) and 0.4–0.6% when they are omitted from the total catch numbers (dry season: 7.180 ind./m<sup>2</sup>, rainy season: 7.777 ind./m<sup>2</sup>). In the mineral subsoil (7–

14 cm depth), the abundance of palpigrads was lower during the dry season (33% of the total catch; 9.6 ind./m<sup>2</sup>) but higher during the rainy season (78% of the total catch; 33.7 ind./m<sup>2</sup>) when compared to the top 7 cm.

A third study was conducted in 1988 in a primary forest on white sand soil, about 45 km north of Manaus (Adis et al. 1989a,b). Palpigrads represented 0.1–0.2% of the total arthropods when Acari and Collembola are included (dry season: 57.703 ind./m<sup>2</sup>, rainy season: 74.255 ind./m<sup>2</sup>) and 0.5–0.9% when they are omitted from the total catch numbers (dry season: 14.119 ind./m<sup>2</sup>, rainy season: 15.023 ind./m<sup>2</sup>). The abundance of palpigrads in the mineral subsoil (7–14 cm depth) was higher during the dry season (86% of the total catch; 57.8 ind./m<sup>2</sup>) and during the rainy season (89% of the total catch; 120.3 ind./m<sup>2</sup>) when compared to the top 7 cm.

To which depth *E. janetscheki* occurs in the soil of the Central Amazonian upland forests is unknown. First studies below 14 cm soil depth in a primary forest on yellow latosol and on white sand soil 45 km north of Manaus showed that soil layers in 20–30 cm depth were dominated by social insects, in particular Isoptera. Palpigradi were not found below 10 cm soil depth, probably due to handsorting of the soil samples (Harada & Bandeira 1994a,b). In Costa Rica, palpigrads were found during the rainy season in 15–20 cm soil depth with abundances of 350 ind./m<sup>2</sup> in a forest and 75 ind./m<sup>2</sup> in a coffee plantation. They represented 1.4% (800 ind./m<sup>2</sup>) and

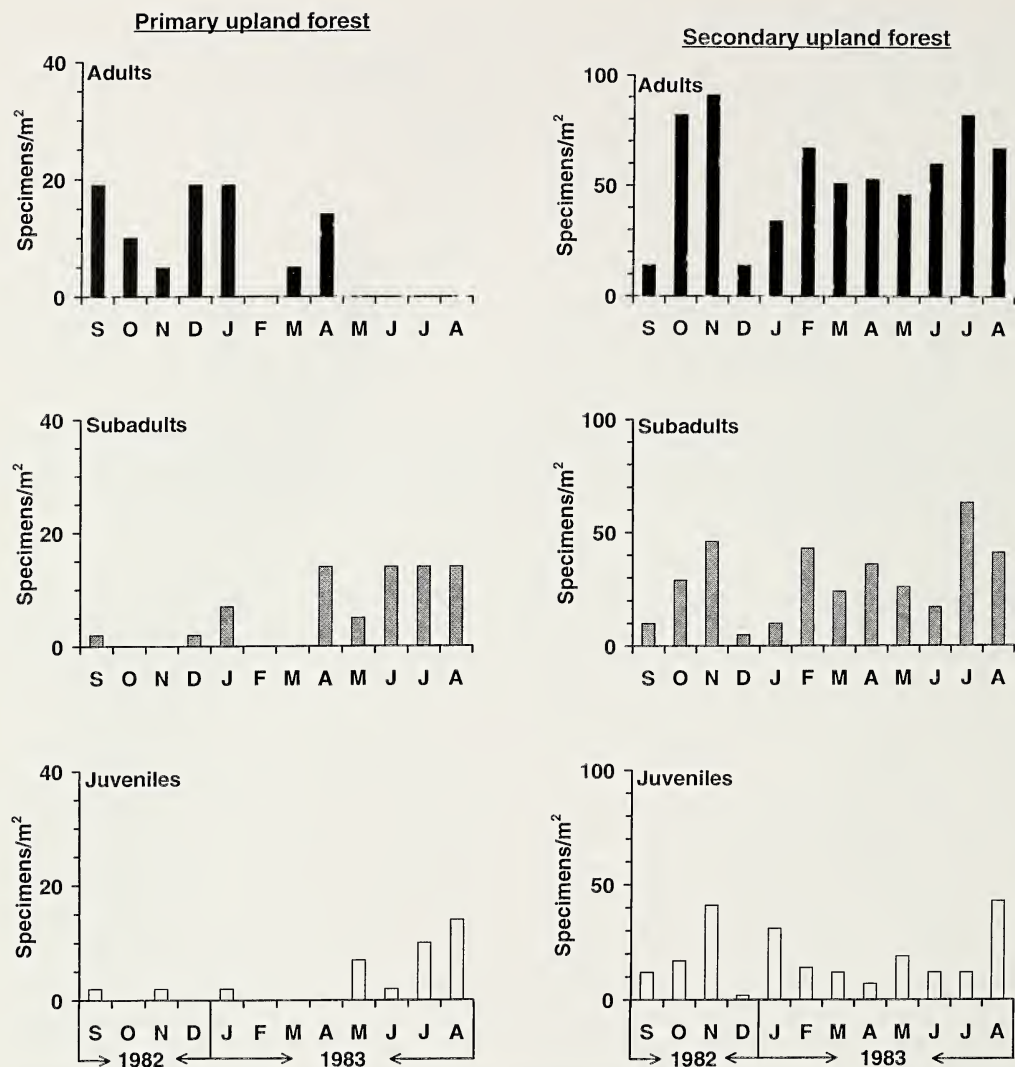


Figure 3.—Temporal occurrence of developmental stages of *Eukoենia janetscheki* in the soil (N/m<sup>2</sup> in 0–7 cm depth) in two upland forests types near Manaus. Monthly samples taken between September 1982 and August 1983.

0.3% (188 ind./m<sup>2</sup>) of the total arthropods collected to a depth of 20 cm, respectively (Serafino & Merino 1978). In Israel, *Eukoենia mirabilis* (Grassi & Calandruccio 1885) was sampled to a soil depth of 15 cm in pine and oak forests. The 71 ind./m<sup>2</sup> represented 0.07% of the total microarthropods obtained (Broza et al. 1993). In Californian pine forests paligrads were detected to a depth of 1.18 m (Price 1975).

The absence of *E. janetscheki* in samples from ground photo-electors in Central Amazonia also indicates that the species is not active on the soil surface. This conclusion is

supported by another study in the primary upland forest at Reserva Ducke, in which no specimens were collected in 20 baited pitfall traps and in three or more ground photo-electors during a sample period of 12 month (Penney & Arias 1982).

Paligrads are considered to be hygrophilous, photophobic, euedaphic inhabitants of soils or troglobites (Condé 1986, 1996; Janetschek 1957; Mahnert & Janetschek 1970; Gruner 1993). *E. janetscheki* was not found in the soil of man-made pastures (0–14 cm depth) adjacent to upland forests in Central Amazonia. One reason might be the low hu-



midity and high temperature of the soil around noon, particularly during the dry season (Adis & Franklin, unpubl. data). The abundance of *E. janetscheki* in the mineral subsoil of the primary upland forest at Reserva Ducke and of the secondary upland forest at Rio Tarumã Mirim was influenced by both abiotic factors. Serafino & Merino (1978) found no palpi-grads in the soil of a pasture in Costa Rica as well.

*E. janetscheki* was also not found in Central Amazonian inundation forests (Adis & Schubart 1984, Adis & Ribeiro 1989). The presence of non-winged terricolous arthropods in this biotope requires flood resistance, horizontal migration according to the high-water line or vertical migration onto the trunk or into the canopy in response to annual flooding of 5–7 months duration. Reproduction cycle and duration of life stages have to be synchronized with the periodic fluctuations in water-level (Adis 1997; Adis et al. 1988, 1997b). At present, our field data indicate that *E. janetscheki* does not meet two of these premises: the species was not collected on or above the soil surface and it had no distinct reproductive period.

A predominance of females over males was reported for the European palpigrad species *Eukoenenia mirabilis* (Gruner 1993; Condé 1996). In *E. janetscheki* almost twice as many females as males were captured in the primary upland forest at Reserva Ducke. The number of females in three species of Symphyla from the same forest and from the secondary upland forest at Rio Tarumã Mirim was even 2–4 times higher than of males (Adis et al. 1997b). Predominance of females assures the continuation of a species, and it probably increases the chance to locate spermatophores deposited by males in the soil.

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## GROUND-LAYER SPIDERS (ARANEAE) OF A GEORGIA PIEDMONT FLOODPLAIN AGROECOSYSTEM: SPECIES LIST, PHENOLOGY AND HABITAT SELECTION

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**ABSTRACT.** Monthly pitfall trapping in 1990 and 1991 at Horseshoe Bend Experimental Area, Clarke County, Georgia, yielded 112 species of spiders belonging to 25 families. Examination of additional collections brings the site total to 145 species in 26 families, including southern or southeastern range extensions for *Agelenopsis kastoni*, *Sphodros atlanticus*, *Bathypantes pallidus*, *Eridantes erigonoides*, *Floricomus tallulae*, *Grammonota inornata*, and *Walckenaeria carolina*, and a northeastern range extension for *Paratheridula perniciosus*. *Ceraticelus emertoni* and *Neriene redacta* are also reported from Georgia for the first time. The proportional distribution of pitfall-trapped species within families does not differ significantly from that reported for Berry's (1966) pitfall trapping in the North Carolina Piedmont (about 450 km away), suggesting regional similarity of the Piedmont ground-layer spider fauna. Data on phenology and relative catch of species among the four habitats sampled (conventional and no-tillage agricultural fields, grassy field borders, and the surrounding deciduous riparian forest) are given for the most abundant species. Habitat selection of 15 abundant species was statistically analyzed; most of the species' populations displayed strong preferences for particular habitats. It is clear that species "spillover" from adjacent habitats contributes to the faunal richness of each habitat, and that maintenance of a mosaic of habitats within an agroecosystem landscape maximizes spider biodiversity.

Since Chamberlin & Ivie's (1944) seminal effort, little work has been conducted on the ground-layer spider fauna of the southeastern Piedmont Plateau region, the mid-elevation area located between the Appalachian Mountains and the Atlantic Coastal Plain. One notable exception is Berry's (1966, 1970) study of the old-field succession of the North Carolina Piedmont, which lists 331 species from the region, including 217 (66%) from over 10,000 pitfall trap/days. The present work reports on the spiders collected during ecological research conducted at Horseshoe Bend Experimental Area, a mosaic of agricultural plots and forest on the floodplain of the Oconee River on the Georgia Piedmont.

In order to better understand the distribution of spiders within the various habitats of this agroecosystem, systematic pitfall trapping was conducted in four distinct (but adjacent) habitats: (1) the natural floodplain forest, undisturbed by management practices, (2) con-

ventional tillage agricultural fields, (3) no-tillage agricultural fields, and (4) the grassy field borders that surround these habitats. Although the four habitat types at Horseshoe Bend are rather small and in close proximity (all within 10 m of each other), they are typical of the modern fragmented landscape of Georgia. Much of the cultivated land in the Georgia Piedmont consists of small plots with a high proportion of "edge" (Turner & Ruscher 1988).

The Horseshoe Bend agricultural fields are planted in grain sorghum in the summer and in winter-rye and crimson clover in the winter. Blumberg (1979) examined ground-layer spiders in these systems at Horseshoe Bend as part of an overall arthropod community characterization, but the low sampling intensity and broad scope of the study meant that the spider assemblages were not extensively characterized and analyzed. The only other study of spiders in grain sorghum is Bailey & Chada's (1968) work describing assemblages in Oklahoma. Blumberg (1979) and this study remain the only examinations of grain sor-

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ghum spider assemblages in the southeastern United States.

The Horseshoe Bend site might be expected to harbor a fairly high diversity of species. The floodplain on which the site is located is a mesic, highly productive site, and the fairly undisturbed floodplain forest is now a rather uncommon habitat in the Georgia Piedmont. The north-facing slopes of the Oconee River harbor a flora (e.g., beech, *Fagus grandifolia*) more characteristic of forests farther north (F.B. Golley pers. comm.). The various open field habitats increase the site's spatial heterogeneity and plant species diversity. Finally, riparian zones such as Horseshoe Bend's floodplain forest may serve as corridors, allowing organisms that are more eurytopic in the mountains or the coastal plain to extend their ranges into the Piedmont.

The objectives of this work are to list the spiders that occur in various habitats on a Georgia Piedmont floodplain; to compare the resultant data with Berry's (1966) list of North Carolina Piedmont fauna, and with other faunal lists compiled using similar collecting methods; and to present phenology and habitat selection data for some of the most abundantly trapped species at the site.

## METHODS

**Study site and habitats.**—This study was conducted at the University of Georgia's Horseshoe Bend Experimental Area near Athens in Clarke County, Georgia (33°55'52"N, 83°21'04"W). It is located on the floodplain of the Oconee River (elevation 244 m) and much of the 14 ha site is occupied by a deciduous riparian forest. The 2 ha currently occupied by the agricultural plots were used as pasture prior to 1964. Between 1964–1978, studies of old-field succession occupied the site (Blumberg & Crossley 1983). The area is relatively flat (slopes < 3%) and the soil is a well-drained, moderately acidic sandy-clay loam (House & Parmelee 1985). The area is flooded in certain years; one corner of the study area was flooded during a week in the winter of 1990, several months before this study was conducted.

The four habitats sampled are as follows:

**Floodplain forest:** This habitat is a deciduous forest typical of southeastern Piedmont riparian zones. Some areas have not been logged for a considerable period, probably in

excess of 100 years, judging from the diameter of some of the trees (F. Golley pers. comm.), though some of the forest was logged as recently as 50 years ago (P. Hendrix pers. comm.). Dominant trees include sweetgum (*Liquidambar styraciflua*), tulip poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), water oak (*Quercus nigra*), chestnut oak (*Quercus prinus*) and beech (*Fagus grandifolia*). The dominant understory tree is flowering dogwood (*Cornus florida*), and poison ivy (*Toxicodendron radicans*) is abundant in the herbaceous layer.

**Grassy field border:** The agricultural fields are separated from the forest by grassy field borders approximately 5 m wide. These consist mainly of fescue grass (*Festuca* sp.) interspersed with annuals. The field borders are contiguous with larger areas of meadow of up to 15 m width in other areas of the Horseshoe Bend clearing. All meadow areas are maintained by periodic mowing, usually four times during the growing season.

**No-tillage agroecosystem:** Four of the eight 32 × 32 m experimental sub-plots on the site have been maintained as no-tillage agricultural plots since 1978. Sorghum (*Sorghum bicolor*) is grown as a summer crop (approx. June–October), and winter rye (*Secale cereale*) and crimson clover (*Trifolium incarnatum*) are grown as cover crops in the winter (approx. November–May). Major weeds include pigweed (*Amaranthus retroflexus*), sicklepod (*Cassia obtusifolia*), and Johnson grass (*Sorghum halepense*) (Parmelee et al. 1989). At the end of both growing seasons the crop is harvested and the next crop is planted by drilling (summer crop) or by surface broadcasting (winter crop). Lack of disturbance to the soil allows a thick litter layer to build up, creating a very different ground-layer microclimate than in the conventional tillage plots (Hendrix et al. 1986).

**Conventional tillage agroecosystem:** The four conventional tillage plots are maintained under the same crop rotation as are the no-tillage plots. However, after the crops are harvested, the conventional tillage plots are moldboard plowed, disked, rotary tilled, and seeded. At the beginning of each growing season, the conventional tillage plots are essentially bare, exposed soil. Conventional tillage plots are thus the most highly disturbed of the four floodplain habitats, with the forest being



the least disturbed by management practices. No pesticides or irrigation are used on any habitat. For specific dates of plowing, planting, and mowing, see Draney (1992).

**Sampling.**—The ground-layer spider assemblages of the four habitats were sampled with 9.5 cm diameter plastic pitfall traps (Morrill 1975) containing 70% ethanol. Traps were run only during days without significant precipitation. Pitfall traps were run for one 24-hour period approximately once a month from August 1990 to August 1991. Twenty-four hour trapping periods sample fauna equally during all times of the day, avoiding the diel bias that can result in a distorted view of community structure (Costa & Crossley 1991). During the first five trapping periods (August 1990–January 1991), ten pitfall traps were placed in each habitat. To obtain a large enough sample to examine the patterns of spider diversity in the four habitats, the number of pitfall traps in each habitat was increased to 20, starting in February 1991 and continuing for the duration of sampling. Cumulative sampling effort was 760 trap-days, 190 days per habitat. For specific trapping dates, see Draney (1992).

Traps were placed in lines of five traps each, resulting in a stratified-random design. Traps within a line were separated by approximately 5 m. Lines were separated from each other by a randomly-selected distance between 5–15 m. In the agroecosystems and the forest, the first trap of each line was placed 5 m from the habitat boundary and lines continued perpendicular to the habitat boundary. In the grassy field margins, traps were placed approximately in the center of the field margin strips, which were 4–5 m wide. For purposes of data analyses, each five trap pitfall line was pooled as a sample unit.

**Processing of samples.**—All Arachnida (other than Acari) were removed from the samples by visual inspection under a dissecting microscope, and stored in clean 70% ethanol for subsequent identification. Initially, spiders in each sample were sexed (male, female, or immature) and identified to morpho-species. Subsequently, animals were identified to species. Errors in initial morphospecies assignment precluded analysis of phenology and habitat selection for species in certain genera, including *Drassyllus*, *Gnaphosa*, *Scotinella*, *Theridion*, *Meioneta*, and two species of

*Phrurotimpus* (*P. borealis* and *P. emertoni*). Since specimens in many of the original samples were removed for use as voucher material, accurate re-examination of the original samples was not possible.

**Other sources of material.**—In order to include as much of the site's spider fauna as possible, all available material collected from Horseshoe Bend was examined in compiling the species list, although only the above-mentioned pitfall data were used in analyses of phenology and habitat selection. The sources are listed in Table 1.

All material was determined by the author, 1992–1995, except as noted in the acknowledgments. Identifications were confirmed during visits to the National Museum of Natural History and the American Museum of Natural History, 1995–1996. Voucher specimens of all taxa have been deposited at the University of Georgia's Natural History Museum.

**Comparison of pitfall faunas.**—Barnes & Barnes (1955) remains the most comprehensive comparison of southeastern spider assemblages. Their work described the "abstract" spider community which occurs fairly constantly in the broomsedge successional habitats occurring on the southeastern Piedmont, and was the first paper to identify such a predictable spider assemblage (Turnbull 1973; Foelix 1982). Comparison of the pitfall fauna of the present study with that of Berry (1966) could indicate the degree of constancy in the ground-layer Piedmont fauna, at least between two widely separated sites (about 450 km apart) in the region.

Differences in sampling effort and nomenclatural changes in the years since Berry's (1966) work make a direct species-level comparison impossible. However, the faunas can be compared at the level of family by examining the proportion of total species found in each family (Table 2). Family richness (28 vs. 24) varies little between the lists. If forest and field assemblages are similar in structure, function, and biogeographic history throughout the Piedmont region (the abstract community *sensu* Barnes & Barnes 1955), then given families should likewise either be diverse and dominate assemblages in terms of species, or remain species-poor throughout the region. To test this, I compared the proportion of total species found in each family at Horseshoe Bend with the number of species ex-

Table 1.—Spiders of Horseshoe Bend Experimental Area, Clarke County, Georgia. All species were trapped in the trough-type or monthly cup-type pitfall traps run in 1990 and 1991 except those species marked with an \*, which are not considered “pitfall species” and not included in comparisons with other pitfall trap faunas. Sources of specimens are: 1, Collected by J. I. Richardson in 1967. Collection methods not known; 2, Collected by G. Bakelaar, 1975, via vacuum sampling and/or sweepnetting of herbaceous vegetation; 3, Hand collected or observed by M. Draney at various times in 1990 and 1991; 4, Large formalin-filled, trough-like directional pitfall traps (140 × 40 cm) placed at habitat boundaries and operated 26 May–8 July, 1991; 5, Monthly 24-hour cup-type pitfall traps in 1990 and 1991 (total effort = 918 trap/days). prob. = “probably;” adult specimens/male specimens needed to confirm identification. cf. = “near;” specimen may be an individual of that species, but differences from the descriptions indicate that it may belong to a closely related species. Genera within families and families within suborders are listed alphabetically. Nomenclature follows Platnick (1993).

	Source of specimens
<b>Mygalomorphae</b>	
<b>Atypidae</b>	
<i>Sphodros atlanticus</i> Gertsch & Platnick 1980	4
<b>Ctenizidae</b>	
<i>Ummidia audouini</i> (Lucas 1835)	4
<b>Cyrtaucheniidae</b>	
<i>Myrmekiaphila fluvialis</i> (Hentz 1850)	3, 5
<b>Araneomorphae</b>	
<b>Agelenidae</b>	
<i>Agelenopsis kastoni</i> Chamberlin & Ivie 1941	2, 3, 5
<b>Amaurobiidae</b>	
<i>Coras medicinalis</i> (Hentz 1821)	4
<i>Coras</i> sp.	4
<i>Wadotes bimucronatus</i> (Simon 1898)	4, 5
<b>Anyphaenidae</b>	
* <i>Teudis mordax</i> (O. P.-Cambridge 1896)	2
* <i>Wulfla saltabunda</i> (Hentz 1847)	2
<b>Araneidae</b>	
<i>Acacesia hamata</i> (Hentz 1847)	2, 4, 5
* <i>Acanthepeira stellata</i> (Walckenaer 1805)	2, 3
* <i>Araneus bicentenarius</i> (McCook 1888)	3
* <i>Araneus</i> sp.	2
* <i>Araniella displicata</i> (Hentz 1847)	2
* <i>Argiope aurantia</i> Lucas 1833	2, 3
* <i>Cyclosa turbinata</i> (Walckenaer 1841)	1, 2, 3
<i>Gea heptagon</i> (Hentz 1850)	1, 4, 5
* <i>Larinia directa</i> (Hentz 1847)	2
* <i>Micrathena gracilis</i> (Walckenaer 1805)	3
<i>Micrathena mitrata</i> (Hentz 1850)	5
* <i>Micrathena sagittata</i> (Walckenaer 1841)	2
* <i>Neoscona arabesca</i> (Walckenaer 1841)	2, 3
<b>Clubionidae</b>	
<i>Cheiracanthium inclusum</i> (Hentz 1847)	2, 5
<i>Clubiona</i> sp. A	1, 2, 5
* <i>Clubiona</i> sp. B	2
<i>Elaver</i> prob. <i>exceptus</i> (L. Koch 1866)	4
<b>Corinnidae</b>	
<i>Castianeira cingulata</i> (C. L. Koch 1841)	3, 5
<i>Castianeira gertschi</i> Kaston 1945	4, 5
<i>Castianeira longipalpa</i> (Hentz 1847)	4, 5
<i>Castianeira trilineata</i> (Hentz 1847)	4
<i>Trachelas deceptus</i> (Banks 1895)	2, 4, 5



Table 1.—Continued.

	Source of specimens
<b>Ctenidae</b>	
<i>Anahita punctulata</i> (Hentz 1844)	5
<b>Dictynidae</b>	
<i>Dictyna volucripes</i> Keyserling 1881	2, 5
<b>Gnaphosidae</b>	
* <i>Callilepis</i> sp.	2
<i>Cesonia bilineata</i> (Hentz 1847)	2, 4
<i>Drassyllus covensis</i> Exline 1962	5
<i>Drassyllus dixinus</i> Chamberlin 1922	4, 5
<i>Drassyllus eremitus</i> Chamberlin 1922	4
<i>Drassyllus ellipes</i> Chamberlin & Gertsch 1940	4
<i>Drassyllus novus</i> (Banks 1895)	5
<i>Gnaphosa fontinalis</i> Keyserling 1887	4, 5
<i>Gnaphosa sericata</i> (L. Koch 1866)	3, 4, 5
<i>Sergiolus ocellatus</i> (Walckenaer 1837)	1, 4
<i>Zelotes aiken</i> Platnick & Shadab 1983	3, 4, 5
<i>Zelotes duplex</i> Chamberlin 1922	4
<b>Hahniidae</b>	
<i>Neoantistea agilis</i> (Keyserling 1887)	5
<i>Neoantistea riparia</i> (Keyserling 1887)	5
<b>Linyphiidae</b>	
<b>Erigoninae</b>	
<i>Ceraticelus emertoni</i> (O. P.-Cambridge 1874)	1, 5
<i>Ceratinella brunnea</i> Emerton 1882	5
<i>Ceratinops crenatus</i> Emerton 1882	5
<i>Eperigone fradeorum</i> (Berland 1932)	4, 5
<i>Eperigone inornata</i> Ivie & Barrows 1935	5
<i>Eridantes erigonoides</i> (Emerton 1882)	4, 5
<i>Erigone autumnalis</i> Emerton 1882	1, 4, 5
<i>Floricomus tallulae</i> Chamberlin & Ivie 1944	5
<i>Floricomus</i> sp.?	5
<i>Goneatara platyrhinus</i> (Crosby & Bishop 1927)	5
<i>Grammonota inornata</i> Emerton 1882	5
<i>Idionella sclerata</i> (Ivie & Barrows 1935)	5
<i>Walckenaeria carolina</i> Millidge 1983	5
<i>Walckenaeria spiralis</i> (Emerton 1882)	4, 5
<b>Linyphiinae</b>	
<i>Bathypantes pallidus</i> (Banks 1892)	4, 5
<i>Centromerus latidens</i> (Emerton 1882)	5
<i>Florinda coccinea</i> (Hentz 1850)	1, 3, 4, 5
<i>Frontinella pyramitela</i> (Walckenaer 1841)	1, 3, 4, 5
<i>Lepthyphantes sabulosus</i> (Keyserling 1886)	5
<i>Meioneta angulata</i> (Emerton 1882)	5
<i>Meioneta barrowsi</i> Chamberlin & Ivie 1944	5
<i>Meioneta</i> cf. <i>leucophora</i> Chamberlin & Ivie 1944	5
<i>Meioneta</i> cf. <i>longipes</i> Chamberlin & Ivie 1944	5
<i>Meioneta micaria</i> (Emerton 1882)	5
<i>Meioneta</i> cf. <i>meridionalis</i> (Crosby & Bishop 1936)	5
<i>Meioneta serrata</i> (Emerton 1909)	5
<i>Neriere radiata</i> (Walckenaer 1841)	5
<i>Neriere redacta</i> Chamberlin 1925	1, 5
<i>Neriere variabilis</i> (Banks 1892)	5
<i>Tennesseelum formicum</i> (Emerton 1882)	4, 5

Table 1.—Continued.

	Source of specimens
<b>Liocranidae</b>	
<i>Agroeca</i> prob. <i>pratensis</i> Emerton 1890	5
<i>Phrurotimpus alarius</i> (Hentz 1847)	4, 5
<i>Phrurotimpus borealis</i> (Emerton 1911)	3, 4, 5
<i>Phrurotimpus emertoni</i> (Gertsch 1935)	4, 5
<i>Scotinella fratrella</i> (Gertsch 1935)	5
<i>Scotinella redempta</i> (Gertsch 1941)	5
<b>Lycosidae</b>	
<i>Allocosa funerea</i> (Hentz 1844)	3, 4, 5
<i>Gladicosa gulosa</i> (Walckenaer 1837)	1, 5
<i>Hogna lenta</i> (Hentz 1844)	2, 3, 5
<i>Hogna timuqua</i> (Wallace 1942)	3, 4, 5
<i>Pardosa atlantica</i> Emerton 1913	2, 3, 4, 5
<i>Pardosa milvina</i> (Hentz 1844)	4, 5
<i>Pardosa pauxilla</i> Montgomery 1904	4, 5
<i>Pirata iviei</i> Wallace & Exline 1978	1, 4, 5
<i>Rabidosa rabida</i> (Walckenaer 1837)	3, 4, 5
<i>Schizocosa ocreata</i> (Hentz 1844)	4, 5
<i>Schizocosa</i> prob. <i>bilineata</i> (Emerton 1885)	5
<b>Oxyopidae</b>	
* <i>Oxyopes aglossus</i> Chamberlin 1929	2
<i>Oxyopes salticus</i> Hentz 1845	1, 2, 3, 4, 5
<i>Peucetia viridans</i> (Hentz 1832)	2, 3, 4
<b>Philodromidae</b>	
* <i>Philodromus imbecillus</i> Keyserling 1880	2
* <i>Philodromus</i> sp. A	2
* <i>Thanatus formicinus</i> (Clerck 1757)	1
<i>Tibellus duttoni</i> (Hentz 1847)	1, 4
<b>Pisauridae</b>	
<i>Pisaurina mira</i> (Walckenaer 1837)	3, 5
<b>Salticidae</b>	
<i>Corythalia canosa</i> (Walckenaer 1837)	4, 5
<i>Habrocestum parvulum</i> (Banks 1895)	4, 5
<i>Habronattus coecadus</i> (Hentz 1846)	2, 5
* <i>Maevia inclemens</i> (Walckenaer 1837)	2
<i>Marpissa lineata</i> (C. L. Koch 1848)	4
* <i>Marpissa pikei</i> (Peckham & Peckham 1888)	2
* <i>Metaphidippus galathea</i> (Walckenaer 1837)	2
<i>Metaphidippus sexmaculatus</i> (Banks 1895)	2, 4, 5
<i>Phidippus audax</i> (Hentz 1845)	2, 3, 4
* <i>Phidippus princeps</i> (Peckham & Peckham 1883)	2
* <i>Phidippus rimator</i> (Walckenaer 1837)	1, 2
* <i>Sarinda hentzi</i> (Banks 1913)	1
<i>Sitticus cursor</i> Barrows 1919	4, 5
<i>Sitticus</i> prob. <i>magnus</i> Chamberlin & Ivie 1944	5
<i>Thiodina puerpura</i> (Hentz 1846)	2, 4
<i>Zygoballus sexpunctatus</i> (Hentz 1845)	2, 4
<b>Segestriidae</b>	
<i>Ariadna bicolor</i> (Hentz 1842)	5
<b>Tetragnathidae</b>	
<i>Glenognatha foxi</i> (McCook 1893)	3, 4, 5
<i>Pachygnatha tristriata</i> C. L. Koch 1845	4
<i>Tetragnatha laboriosa</i> Hentz 1850	2, 3, 4
<i>Tetragnatha straminea</i> Emerton 1884	2, 4



Table 1.—Continued.

	Source of specimens
<b>Theridiidae</b>	
<i>Argyrodes lacerta</i> (Walckenaer 1841)	5
<i>Dipoena nigra</i> (Emerton 1882)	5
<i>Latrodectus mactans</i> (Fabricius 1775)	3, 5
<i>Paratheridula pernicioso</i> (Keyserling 1886)	5
<i>Pholcomma hirsutum</i> Emerton 1882	5
<i>Phoroncidia americana</i> (Emerton 1882)	5
<i>Steatoda americana</i> (Emerton 1882)	5
<i>Stemmops ornatus</i> (Bryant 1933)	5
<i>Theridion</i> (2–3 spp.)	5
<i>Theridula opulenta</i> (Walckenaer 1841)	1, 2, 4
<b>Thomisidae</b>	
* <i>Misumena vatia</i> (Clerck 1757)	1, 2
* <i>Misumenoides formosipes</i> (Walckenaer 1837)	1, 2
* <i>Misumenops</i> (2 spp.)	2
* <i>Synema parvulum</i> (Hentz 1847)	1
* <i>Tmarus angulatus</i> (Walckenaer 1837)	2
<i>Xysticus ferox</i> (Hentz 1847)	1, 2, 3, 4, 5
<i>Xysticus triguttatus</i> Keyserling 1880	2, 4, 5
<i>Xysticus</i> sp.	4, 5
<b>Uloboridae</b>	
<i>Uloborus glomosus</i> (Walckenaer 1841)	3, 4
<b>Zoridae</b>	
<i>Zora punila</i> (Hentz 1850)	4

pected in each family based on the proportional representation of the Berry (1966) data via a Chi-square test ( $\alpha = 0.05$ ; Table 3). For both lists, species identified only to genus were included only if no congener exists in the same list. Placement of species within families follows Platnick (1993) rather than Berry's (1966) original placement. In order to account for rare families that were not present in both lists, I lumped species from all families representing < 5% of species richness of the Berry (1966) data into a single "other families" category.

If there is a similarity of ground-layer faunas throughout the Piedmont region, it is expected that the structure of the Horseshoe Bend fauna would be more similar to the Piedmont fauna of Berry (1966) than to pitfall fauna of other regions. I examined this by comparing the fauna of the present study to six other complete lists of pitfall spider species from outside the Piedmont Plateau region (Table 3) using the same chi-square test procedure.

**Data analysis.**—In comparing the Horseshoe Bend fauna with other faunas, only the pitfall samples are included, due to the un-

quantifiable and uneven collecting of vegetation-layer spiders. The 1990–91 pitfall collections (cup and trough traps) together represent a significant portion of the total spider diversity sampled at the site, including 112 species (77% of Horseshoe Bend total) belonging to 25 families, of which 71 species (63% of pitfall fauna) were sampled only with these methods.

For examining phenological patterns, data representative of the entire year without temporal bias are preferable. The phenology data set consists of 10 traps per habitat-date for all dates, August 1990–August 1991, and includes 960 adult spiders trapped over 480 trap/days.

To ensure taxonomic accuracy, only adult spiders were included in examining species' habitat preferences. In order to maximize sample size while avoiding temporal bias in sampling effort, only months with 20 pitfall traps (February–August 1991) were included in the data set from which habitat selection information was extracted. Each habitat was sampled with four 5-pitfall sample units on each of seven dates, giving 28 samples at each hab-

Table 2.—Comparison of Horseshoe Bend pitfall fauna with North Carolina Piedmont pitfall fauna listed in Berry (1966). Only species captured in pitfalls in the piedmont are recorded for Berry (1966). Taxa identified only to “sp.” were included only if no congener was listed. Families are listed in descending order of species richness of the Horseshoe Bend fauna, with ties listed alphabetically.

Family	Number of species		% in this study	% in Berry 1966
	(this study)	(Berry 1966)		
Linyphiidae	29	47	25.89	21.66
Gnaphosidae	11	17	9.82	7.83
Lycosidae	11	34	9.82	15.67
Salticidae	10	23	8.93	10.60
Theridiidae	10	12	8.93	5.53
Liocranidae	6	6	5.36	2.76
Corinnidae	5	3	4.46	1.38
Tetragnathidae	4	4	3.57	1.84
Araneidae	3	16	2.68	7.37
Clubionidae	3	2	2.68	0.92
Thomisidae	3	11	2.68	5.07
Amaurobiidae	2	2	1.79	0.92
Hahniidae	2	4	1.79	1.84
Oxyopidae	2	4	1.79	1.84
Agelenidae	1	4	0.89	1.84
Atypidae	1	1	0.89	0.46
Ctenidae	1	0	0.89	0.00
Ctenizidae	1	1	0.89	0.46
Cyrtacheniidae	1	1	0.89	0.46
Dictynidae	1	5	0.89	2.30
Philodromidae	1	5	0.89	2.30
Pisauridae	1	3	0.89	1.38
Segestriidae	1	1	0.89	0.46
Uloboridae	1	0	0.89	0.00
Zoridae	1	1	0.89	0.46
Anyphaenidae	0	5	0.00	2.30
Mimetidae	0	1	0.00	0.46
Mysmenidae	0	1	0.00	0.46
Nesticidae	0	1	0.00	0.46
Oonopidae	0	1	0.00	0.46
Titanoecidae	0	1	0.00	0.46
Total species	112	217	100.00	100.00
Total families	25	29		

itat. This data set consists of 1436 adult spiders trapped over 560 trap/days.

Data from each of 15 species in which at least 20 adults were trapped were analyzed separately by 2-Way ANOVA, with habitat as the major predictive variable and blocked by sample date. Data showing a significant among-habitat effect were subjected to a uni-

variate ANOVA and habitat means separation via Fisher’s LSD.

RESULTS AND DISCUSSION

**The Horseshoe Bend spider fauna.**—In all, 145 spider species belonging to 26 families have been collected at Horseshoe Bend (Table 1). This list represents the most extensive pitfall trapping survey yet conducted on the Georgia Piedmont. Note, however, that species collected only in 1967 and/or 1975 should be viewed with caution, as the collections were made in old field successional habitats that are largely absent from the site today.

A Chi-square test showed that the observed proportional distribution of species within families was not significantly different from the distribution predicted based on the Berry (1966) list (Table 3). Thus, the two faunas have similar family-level structure, which is consistent with the concept of an abstract Piedmont ground-layer assemblage.

In contrast to the Piedmont fauna comparison, the species-within-families distribution of the Horseshoe Bend fauna was significantly different ( $\alpha = 0.05$ ) from each of the six non-Piedmont faunas (Table 3). While the above does not constitute a rigorous test of the hypothesis that there exists an “abstract Piedmont ground-layer spider assemblage”, it is at least consistent with such a hypothesis, and suggests some broad regional similarity of ground-layer spider faunas at the level of family.

**Range extensions.**—The pitfall data include records of new range extensions for eight species. Seven of these are southern or southeastern and one is a northeastern range extension. The predominance of southern over northern range extensions at this site is not surprising considering: 1) the site is located near the southeastern corner of the continent, so much more land occurs to the north and west of this site than to the south and east, and 2) much more spider collecting has been conducted to the north of this area, due to the historical distribution of arachnologists in the midwest and middle and northern Atlantic states.

*Agelenidae: Agelenopsis kastoni* Chamberlin & Ivie 1941: Two males were captured in the forest on 26–27 March and another male on 23–24 April 1991. Few collection localities of this spider have been published since



Table 3.—Results of Chi-square test ( $\alpha = 0.05$ ) of hypothesis that distribution of pitfall spider species richness between families is similar between present study and other faunas. Comparison studies are listed in descending order by number of families.

Study	Location	Habitats
Present study	Georgia Piedmont	Riparian fields and forest
Berry 1966	North Carolina Piedmont	Forests and old fields
Muma 1973	Central Florida	Pine, citrus, residential
Bailey & Chada 1968	Oklahoma	Grain sorghum
Muma 1975	New Mexico	Desert grassland, sand dunes
Maelfait & DeKeer 1990	Belgium	Grazed pasture, grassy edge
Muma & Muma 1949	Nebraska	Prairie, wooded ravine
Koponen 1992	Northwest Territories, Canada	Various low arctic habitats

Chamberlin & Ivie (1941) described the species from single male and females types from Haddam, Connecticut. It is known from Oconee and Pickens Counties, South Carolina (Gaddy & Morse 1985), and was listed in Berry (1966) as a North Carolina Piedmont pitfall spider, also collected in forest. The Horseshoe Bend records extend the known range of the species at least 50 km south. Recently, four males were trapped on the inner coastal plain as well, extending the known range even farther south (South Carolina: Barnwell County, Savannah River Site; Set-Aside #29, Scrub Oak Natural Area, 17 April–3 May 1996. Coll./Det. M. Draney).

*Atypidae: Sphodros atlanticus* Gertsch & Platnick 1980: One male was captured in a trough trap between the forest and the grassy field border during the last week of June 1991. Another male was trapped one week later at the edge of the sorghum field, about 75 m from the forest edge, where the spider presumably originated. Hall County, Georgia is the previous southernmost collection record; these specimens extend the known range of the species southward by about 40 km. Other localities reported for *S. atlanticus* are Jackson County, Illinois; Carteret and Jackson Counties, North Carolina; and Spotsylvania County, Virginia (Gertsch & Platnick 1980; Coyle et al. 1985). Berry's (1966, 1970) list does not include *S. atlanticus* but lists *Sphodros niger* (Emerton) (listed as *Atypus*); however, like many of the taxa on the present list, *Atypidae* was revised and *S. atlanticus* described since the publication of Berry's (1966, 1970) list (Gertsch & Platnick 1980).

*Linyphiidae: Bathyphantes pallidus* (Banks

1892): Seven adult individuals of this species were captured in the no-tillage and grassy field border habitats in March, May, June, July and September 1991. The species is widely distributed across the United States to about 34° N, with the southernmost localities at Highlands and Clingman's Dome, North Carolina (Ivie 1969). The Horseshoe Bend records extend the known range of the species southward by about 120 km. However, a single female was recently trapped even further south on the inner coastal plain (South Carolina: Aiken County; Jackson. Deciduous woods behind 110 Cowden St.; Pitfall, 12–16 March 1995. Coll./Det. M. Draney). These are the southernmost records for the genus, except that an undetermined species of *Bathyphantes* was reported from Florida (Anonymous 1986).

*Linyphiidae: Eridantes erigonoides* (Emerton 1882): This species is common in the no-tillage fields at Horseshoe Bend, where 31 of the 38 adults were captured (Table 4, Fig. 6). It has previously been collected in several states north of Georgia, including Maryland, Tennessee, Virginia, and the District of Columbia (Roth et al. 1988). It is absent from Berry's (1966, 1970) list. The Horseshoe Bend records are the southernmost known, except that a male and female were trapped further south on the upper coastal plain (South Carolina: Barnwell County; Savannah River Site. Pipeline cut with brambles and *Prunus*; Sifting litter, 28 October 1994. Coll./Det. M. Draney).

*Linyphiidae: Floricomus tallulae* Chamberlin & Ivie 1944: Two females were trapped in February and seven males in April 1991 in the

Table 3.—Extended.

Species	Families	Significantly different from present study?
112	25	
217	29	No
128	24	Yes
64	17	Yes
45	16	Yes
77	13	Yes
55	13	Yes
22	5	Yes

forest. Chamberlin & Ivie (1944) collected this species (then new to science) from Habersham, Hall, and Rabun Counties, Georgia, with the southernmost collection locality being Gainesville (about 40 km north of Horseshoe Bend). The species is absent from Berry's (1966, 1970) list, and seems not to have been collected since its description.

*Linyphiidae: Grammonota inornata* Emerton 1882: The species is quite common at Horseshoe Bend, where it thrives in the no-tillage fields (Table 4, Fig. 9). The species is

known from states north of Georgia, including North Carolina, Tennessee, and Virginia. The records at this site confirm that it thrives in Georgia, but the southern range extension is provided by a male found in the UGA Natural History Museum from the outer coastal plain (Georgia: Tift County; Tifton; Oatfield sweep, December 1963–January 1964. Coll. R. Davis, Det. H.E. Frizzell, examined).

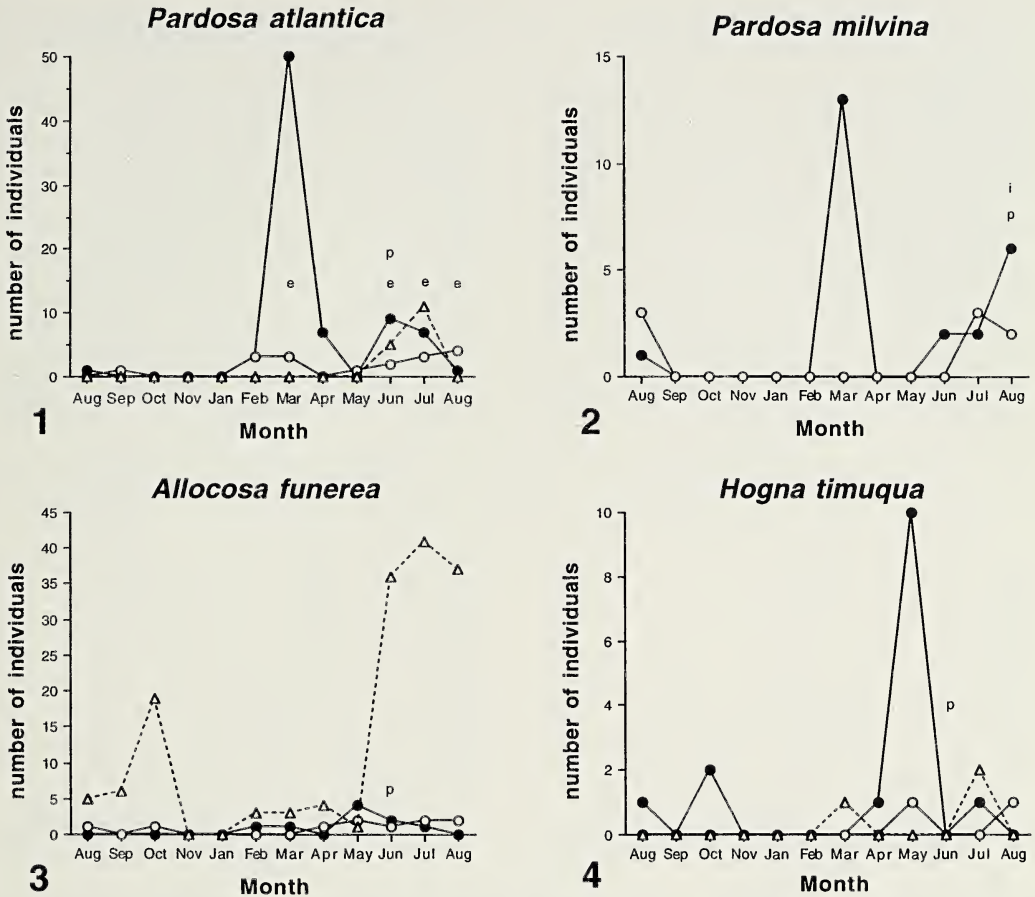
*Linyphiidae: Walckenaeria carolina* Millidge 1983: A single male was trapped in conventional tillage winter rye/crimson clover in January 1991. Prior to my finds, it was known from only a few localities in Missouri, North Carolina and West Virginia. This species was described recently (Millidge 1983, holotype collected by J. Berry at Durham, North Carolina), so range extensions are not surprising. The species appears to be common on the inner coastal plain; over 60 individuals of this species were trapped in various habitats in Aiken, Barnwell, and Allendale Counties, South Carolina during 13 December 1995–21 February 1996 (Coll./Det. M. Draney).

*Theridiidae: Paratheridula pernicios*a (Keyserling 1886): Several specimens of both sexes were taken in June, July and August 1991 in the conventional tillage field ( $n = 4$ )

Table 4.—Habitat selection of 15 abundant pitfall species. Table includes all taxa in which at least 20 adults were trapped in 7 monthly 24-hour trap periods of 20 traps/habitat (total = 560 trap/days). Taxa are listed in descending order of number of adults trapped. Habitat abbreviations: C = Conventional tillage field; N = No-tillage field; G = Grassy field borders; F = Floodplain forest. Significance levels: \*  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.0001$ . ns = Not significant at  $\alpha = 0.05$ .

Species	Total adults	Adults in each habitat				Habitat 1-way ANOVA means separation	2-Way ANOVA		M-H interaction
		C	N	G	F		Habitat	Month	
<i>Erigone autumnalis</i>	212	61	48	103	0	G > C, N > F	***	**	ns
<i>Pardosa atlantica</i>	175	78	67	30	0	C > G, F; N > F	***	***	***
<i>Glenognatha foxi</i>	137	65	66	6	0	C, N > G, F	***	***	***
<i>Grammonota inornata</i>	104	11	84	6	3	N > C, G, F	***	**	***
<i>Pardosa milvina</i>	55	38	5	12	0	C > N, G, F	***	***	***
<i>Idionella sclerata</i>	46	0	2	40	4	G > C, N, F	**	ns	ns
<i>Eridantes erigonoides</i>	38	1	31	6	0	N > C, G, F	***	ns	ns
<i>Phrurotimpus alarius</i>	34	0	3	0	31	F > C, N, G	***	***	***
<i>Allocosa funerea</i>	31	3	8	20	0	G > C, N, F; N > F	***	***	*
<i>Ceraticelus emertoni</i>	30	4	1	23	2	G > C, N, F	***	ns	*
<i>Eperigone fradeorum</i>	30	15	1	12	2	C > N, F; G > N	**	**	ns
<i>Hogna timuqua</i>	26	5	15	5	1	N > C, G, F	**	***	ns
<i>Neoantistea agilis</i>	26	0	3	8	15	F > C, N	**	***	ns
<i>Tennesseelum formicum</i>	23	12	2	6	3	C > N, F	**	ns	**
<i>Pirata iviei</i>	20	2	5	11	2	No differences	ns	*	ns





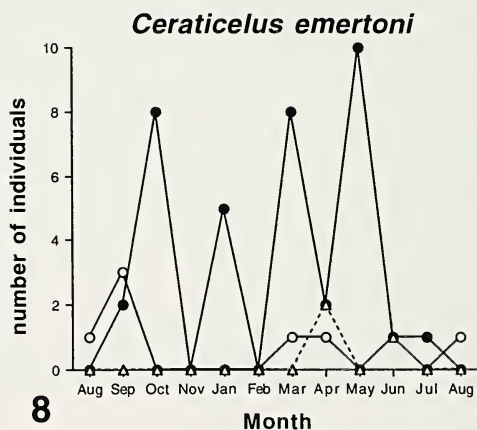
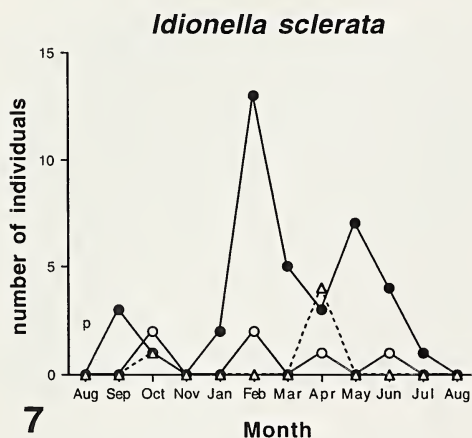
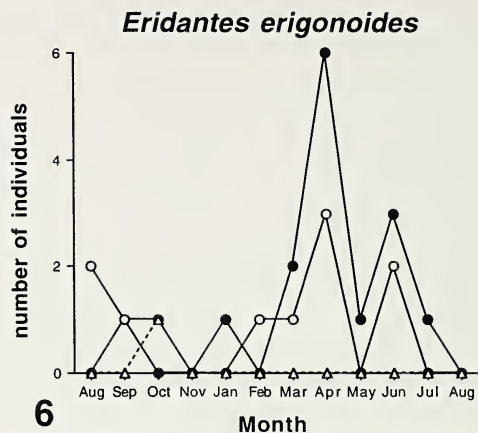
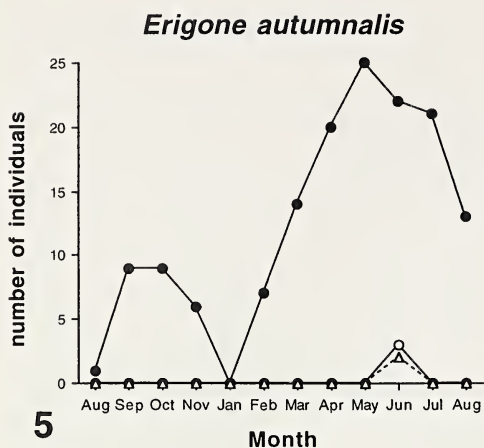
Figures 1–4.—Phenograms of four spider species, family Lycosidae. Graphs illustrate numbers of each stage trapped in 40 traps (10 in each of four habitats) during each of 12 monthly 24-hour trapping periods. Closed circles (●) = males; open circles (○) = females; triangles (Δ) = immatures; “p” = penultimate instar males; “e” = egg sac; “i” = immatures on female.

and the grassy field borders ( $n = 1$ ). This species is most commonly collected on the outer coastal plain of the gulf coast states, and has been found as far north as Tuscaloosa, Alabama (Levi 1957, as *P. quadrimaculata* (Banks)). The Horseshoe Bend records are a northeastern range extension for the species, which was not listed in Berry (1966, 1970).

Besides the three species noted above, several other Horseshoe Bend species were also missing from Berry’s (1966) list, including *Castianeira gertschi*, *Neriene redacta*, *Ceraticelus emertoni*, *Eperigone inornata*, and *Idionella sclerata*. Of these, *C. gertschi* and *I. sclerata* are recorded from North Carolina and *C. emertoni* probably occurs there, having been recorded from Virginia (Reiskind 1970; Roth et al. 1988). The remaining five species

not yet recorded from North Carolina represent less than 5% of the Horseshoe Bend pitfall fauna (Table 1), indicating the high degree of similarity of the Piedmont fauna of North Carolina and Georgia. Two of these species, *C. emertoni* and *N. redacta*, are also new records for the state of Georgia, although they have been collected in other southeastern states (Roth et al. 1988). Two female *N. redacta* were also collected at the site by J.I. Richardson on 5 September 1967.

**Phenology.**—Twelve spider species were trapped in large enough numbers to give some insight into their life cycles. Phenograms for these species are given in Figs. 1–12. Because pitfall catches reflect the level of activity of a population in addition to its density (Uetz & Unzicker 1976), the numbers trapped should



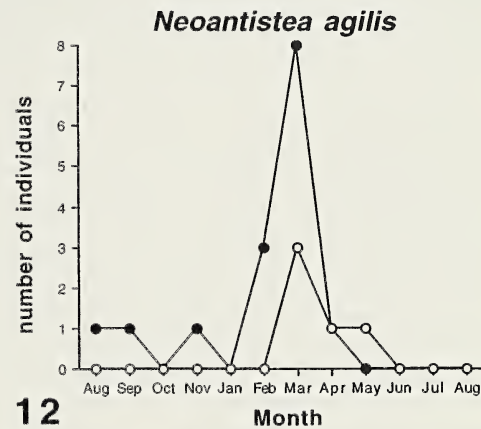
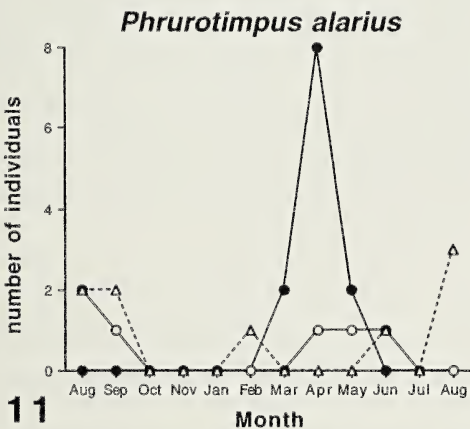
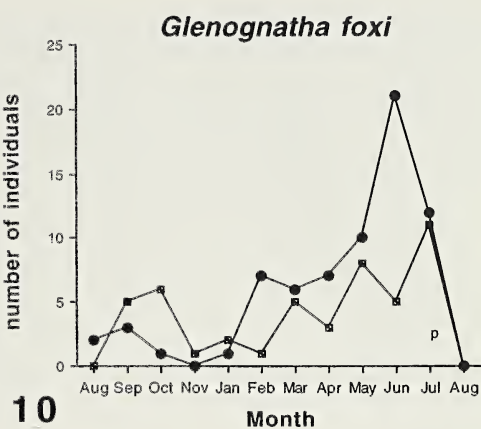
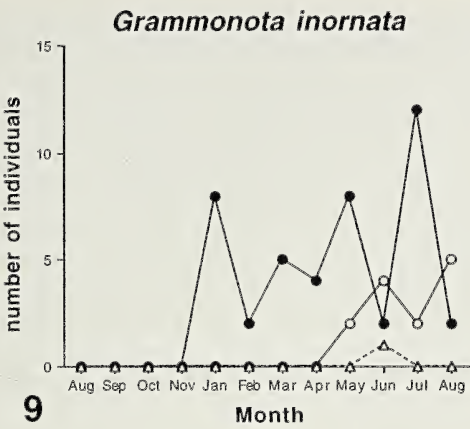
Figures 5–8.—Phenograms of four spider species, family Linyphiidae. Graphs illustrate numbers of each stage trapped in 40 traps (10 in each of four habitats) during each of 12 monthly 24-hour trapping periods. Closed circles (●) = males; open circles (○) = females; triangles (△) = immatures; “p” = penultimate instar males.

not be interpreted as directly reflecting population density during the trapping period. In general, male spiders are most active when searching for mates and female spiders are most active when foraging or searching for oviposition sites just prior to and during the period of egg production. Thus the peaks in pitfall catch can be roughly equated with the periods of copulation and egg production (DeKeer & Maelfait 1987). Assuming that immature spiders are often food limited (Wise 1993) and likely to be actively foraging, pitfall catch can be roughly equated with density of immatures. This is likely to be valid only during the warm season, when the immatures are not in diapause or otherwise inactive.

Phenograms for four abundant lycosid species are given in Figs. 1–4. Note the peak in

male abundance in March for both *Pardosa* species, *P. atlantica* and *P. milvina* (Figs. 1,2). Both species (the two most abundantly trapped lycosids) seem to have an identical “mating season” after which low numbers of adults continue to be captured until August or September and immatures are trapped until October or November. Berry (1971) documents the seasonal distribution of another *Pardosa* species, *P. parvula* Banks (as *P. saxatilis* (Hentz)). His pitfall catches show no adults present in March, followed by two peaks of adults. The first peak, in April, was dominated by males (28:1), but by the second, July, peak almost equal numbers of males and females were captured (76 and 65, respectively; J. Berry unpubl. data). This could indicate a spring “mating season” peak similar to the





Figures 9–12.—Phenograms of four spider species: 9, Linyphiidae; 10, Tetragnathidae; 11, Liocranidae; 12, Hahniidae. Graphs illustrate numbers of each stage trapped in 40 traps (10 in each of four habitats) during each of 12 monthly 24-hour trapping periods. Closed circles (●) = males; open circles (○) = females; triangles (△) = immatures; “p” = penultimate instar males. In Fig. 10, squares (■) represent females and immatures of *Glenognatha foxi*, which could not be reliably separated.

Horseshoe Bend *Pardosa* species, but delayed due to cooler weather than occurred at Horseshoe Bend in 1991 (a warmer than normal year). Berry (1971) states that the weather during his April collecting period was “very cold and wet.” Alternatively, the later peak of *P. parvula* could be due to life history properties intrinsic to the species.

*Allocosa funerea* showed a similar, but less pronounced spring peak of males, but in May instead of March (Fig. 3). A high proportion of *A. funerea* individuals was trapped as immatures, beginning in June. It is unclear whether this indicates that *A. funerea* adults had a particularly successful reproductive season relative to the *Pardosa* species, or whether juveniles of this species are relatively more active or the adults relatively less active than

is the case with the other lycosid species. These three species probably overwinter as large juveniles, then mature and mate in the spring. This pattern seems to be the rule among smaller lycosids in temperature regions (Doane & Dondale 1979).

The larger lycosid *Hogna timuqua* showed a distinct peak of males in May (Fig. 4). This species probably mates in the spring but most likely needs two years to mature instead of one, perhaps overwintering the second winter as adults, as is the case with other large temperate lycosids (Dondale 1977). Immatures of two distinct size classes can be found in the summer (Draney pers. obs.).

Adults of many species of erigonine Linyphiidae were trapped during all seasons of the year (Figs. 5–8). Males of the most commonly

trapped spider species, *Erigone autumnalis* were present in all months except January; the catch peaked in May. The few females and identifiable immatures of this species were trapped in June (Fig. 5). The very skewed sex ratio in the pitfall catch probably indicates that the females are not normally very active on the ground surface. Other erigonines which were trapped during most of the year include *Idionella sclerata* (Fig. 7), *Eridantes erigonoides* (Fig. 6), and *Ceraticelus emertoni* (Fig. 8). The mainly year-round presence of adults and the erratic occurrence of both males and females (no clearly defined peak indicating a "mating season") suggests that these species are probably multivoltine with overlapping generations. This may be the case with *E. autumnalis* as well. Other erigonine species from the southeast are capable of completing their life cycle (egg to egg) in under four months in the lab (Draney unpubl. data), so more than one generation per year is a possibility for these species. One erigonine which seems to display an annual life cycle at Horseshoe Bend is *Grammonota inornata* (Fig. 9). The sequential appearance of males in January, females in May, and identifiable immatures in June, and the absence of any identifiable individuals in the autumn suggests a strong seasonal cycle for this species.

The tetragnathid *Glenognatha foxi* was trapped in all months of the year, with catch increasing from a low in November to a peak in June (Fig. 10). This pattern probably indicates an annual reproductive cycle with mating in the early summer. Alternatively, these small tetragnathids may reproduce throughout the year, with population levels and/or dispersal behavior (thus trap vulnerability) highest in the early summer. Knowing when immature *G. foxi* exist at the site should resolve the question, but I was unable to confidently separate females from immatures in this species, so females and immatures are lumped in the data. Berry (1971) graphed the seasonal distribution of *G. foxi* (as *Mimognatha foxi*) in his pitfalls. His data show low numbers (< 5 individuals/sample date) of adults (males and females pooled) trapped throughout the year, and low numbers of immatures trapped during June through September. The two sets of data together indicate an annual reproductive cycle for this species in the Piedmont region.

Most males of the liocranid *Phrurotimpus alarius* were trapped in April, with immatures and females found at low levels from February to September (Fig. 11). If the hypothesis of an annual cycle with spring mating is correct, then I expect that immatures captured in late winter/early spring would be large subadult specimens, whereas those captured in the summer would be smaller immatures that were produced after the spring mating.

Peck & Whitcomb (1978) present pitfall catch data for *P. alarius* which also support the hypothesis of an annual cycle with spring mating. Their catch of males and females (immatures were not recorded) peaked in May instead of April, which may be consistent with the more northerly Arkansas study site resulting in a delayed "mating season." At the Arkansas site, males disappeared after May, whereas females were trapped through September. This pattern is similar to that shown at Horseshoe Bend, again corroborating my life history hypothesis.

A similar pattern in the hahniid *Neoantistea agilis* is also interpreted as an annual cycle with spring mating (Fig. 12). Males peaked in March and females were trapped from March to May. No immatures were trapped, suggesting that they spend their time within the leaf litter rather than walking on the ground surface. It would be interesting to know whether the few males that were trapped in August-November are old adults that survived to autumn or whether they are newly adult individuals that overwinter as adults. The absence of males in May, June, and July indicate that the latter hypothesis is more likely. *N. agilis* in Manitoba, Canada apparently displays a different life history, with male pitfall peaks in September (Aitchison 1984). Possibly the Manitoba populations are also annual, but a longer period is required for maturation in the cooler climate, so the mating is delayed until Autumn. Opell & Beatty (1976) suggest that the species is annual but has two periods of reproduction, in late March to late May and again in mid-August to mid-September. The species may facultatively reproduce during spring and/or autumn, with climate and other conditions determining the local life history pattern.

**Habitat selection.**—The four habitats sampled at Horseshoe Bend are all within 10 m of one another and adjacent to one another,



except that the grassy field border separates the agricultural from the forest habitats by a few meters. Since all habitats should be easily accessible to all spider species at the site, sampling within the small scale of this agroecosystem landscape enables a determination of the aggregate "habitat preferences" of the spider populations. This requires the assumption that numbers of individuals trapped broadly corresponds to the density of individuals in that habitat. Care must be taken since pitfall trapping data has often been shown to violate this assumption (Uetz & Unzicker 1976; Curtis 1980; Merrett & Snazell 1983; Topping 1993). Most potential sources of bias have been controlled for in this study. Temporal sources of bias were controlled by trapping simultaneously in all habitats for 24 hours at a time. Effects of weather on spider mobility were controlled for by simultaneous trapping at adjacent sites exposed to identical weather conditions. Interspecific variation in trap vulnerability is not relevant in this context because abundance comparisons are only made intraspecifically. I acknowledge that habitat architecture can influence the efficiency of the traps (Topping 1993), and that this factor was not controlled for in this study. Even if habitat architecture does affect pitfall catch, species habitat preference should still be identifiable unless architecture has an overwhelming effect on the trappability of species. Comparing catches of species with presumably similar locomotory abilities suggests that this is not the case. For example, *Grammonota inornata* was abundantly trapped in the no-tillage field and rarely trapped in the grass borders (84 and 6 adults, respectively) whereas another erigone linyphiid, *Idionella sclerata*, showed the opposite pattern (2 and 40 individuals, Table 4). Such examples of independent catches of apparently similar species in different habitats suggests that architecture is at least not the overriding factor determining pitfall catch, and that habitat preference of individual species can be examined despite this potentially confounding variable.

Some trends in habitat selection are suggested by examining the habitats in which the 46 clearly identifiable species in the February-August 1991 data set were trapped. Data for the 15 most abundant of these species are shown in Table 4. One immediately apparent feature is that few species were entirely re-

stricted to a single habitat. Although 37% of the species ( $n = 17$ ) were found in only one habitat, only one species, *Floricomus tallulae* (not in Table 4; forest,  $n = 8$ ) was represented by more than three individuals.

Another interesting feature of the habitat use list concerns those species which were trapped in all habitats except one. Of the 46 species, 24% ( $n = 11$ ) were present in three of the four habitats. Eight of these species avoided the forest: *Eridantes erigonoides*, *Erigone autumnalis*, *Florinda coccinea* (not in Table 4;  $n = 6$ ), *Walckenaeria spiralis* (not in Table 4;  $n = 7$ ), *Allocosa funerea*, *Pardosa atlantica*, *Pardosa milvina*, and *Glenognatha foxi*. The three remaining species all avoided the conventional tillage habitat: *Neoantistea agilis*, *Idionella sclerata*, and *Xysticus triguttatus* (not in Table 4;  $n = 6$ ). These results are consistent with my expectation that the only habitats that are "avoided" by species with otherwise general habitat requirements are the habitats at either end of a gradient from frequently and intensely disturbed and managed (conventional tillage field) to infrequently disturbed (forest). Species are less likely to avoid the intermediate no-tillage field and grassy field border habitats.

Six species (all linyphiids or lycosids) were trapped in all four habitats: *Ceraticelus emertoni*, *Eperigone fradeorum*, *Grammonota inornata*, *Tennesseelum formicum*, *Hogna timuqua*, and *Pirata iviei*. This represents 25% of the 24 species represented by at least four individuals in the data set (and thus theoretically capable of being found in all habitats given their level of activity density). Interestingly, four of the five most abundantly trapped species in Table 4 (*Erigone autumnalis*, *Pardosa atlantica*, *Glenognatha foxi*, and *Pardosa milvina*) did not occur in all four habitats. This is perhaps contrary to Abraham's (1983) assertion that dominant spider species in ecosystems tend to be habitat generalists. At Horseshoe Bend, some of the most abundant species are habitat specialists at least to the extent that they do not occur abundantly in the forest habitat.

Table 4 also presents results of statistical analyses of the habitat distribution of the 15 most abundantly trapped species ( $n > 19$ ). Two-way ANOVA's showed that all species except *Pirata iviei* displayed a significant habitat effect. *Pirata iviei* appears to range widely



in the floodplain habitats, but was not caught in numbers sufficient to show a significant habitat preference. About half of the remaining species showed a significant "month  $\times$  habitat" interaction, implying that the habitat "preference" of the species changed over time. In some cases, this may be a statistical artifact resulting from low capture rate during certain months.

One-way ANOVA's were performed on all data showing a habitat effect when blocked by month in the two-way ANOVA. Means separation by LSD indicated in which habitats the species were trapped significantly more or less often. Most of these abundant species were much more common in one or two habitats than in the remainder, in which they were rarely or never trapped. This pattern of habitat specialization was also observed in Maelfait & De Keer's (1990) study of spiders in pastures and their border zones.

*Forest species:* Only 2 of the 15 abundant species preferred the forest habitat, *Neoantistea agilis* and *Phrurotimpus alarius*. *N. agilis* was rarely trapped in either agricultural habitat and seems to avoid them. Its prevalence in the forest is consistent with previous collection data (Opell & Beatty 1976).

*Field border species:* The thin grassy field borders seem, at first glance, much less a distinct "habitat" than the fields and forest. However, grasslands in Georgia (mostly small strips and patches like the ones in this study) account for about 14% of the land in the state, and can serve as important reservoirs for both beneficial and destructive insects (Morrill 1978). Four species were characteristic of the grassy field borders: the lycosid *Allocosa funerea* and the linyphiids *Ceraticelus emertoni*, *Erigone autumnalis*, and *Idionella sclerata*. *Erigone autumnalis* definitely avoids the forest; none of the 212 individuals were trapped there. Another linyphiid, *Eperigone fradeorum*, was also trapped in considerable numbers in the grassy borders, though it showed a stronger affinity for the conventional-tillage agroecosystem. *Allocosa funerea* was also often trapped in the no-tillage agricultural field. This species has often been collected in grassy fields, meadows, and lawns, in addition to gardens and pine forests (Dondale & Redner 1983).

Duelli (1990) found few species which preferred the grassy margins between cultivated

fields and semi-natural (grassland/pasture) areas, and considered the grassy margins in his system to be ecotones, mainly important for harboring species more common elsewhere. However, I have documented several common spiders that were trapped predominantly in the meadow habitats at Horseshoe Bend, indicating that this is their primary habitat, and does not serve as ecotone for them. The grassy habitats at Horseshoe Bend undoubtedly also serve as secondary habitats for species which are more abundantly trapped in cultivated fields or forest. In particular, the grassy margins may provide a refuge for cultivated field populations during times when that habitat is disturbed by management practices.

*No-tillage field species:* *Hogna timuqua* was trapped in the no-tillage agricultural field significantly more often than in other habitats. Two other lycosids commonly trapped here were *Pardosa atlantica* and *Allocosa funerea*, though both had stronger affinities to other habitats. Two linyphiids, *Eridantes erigonides* and *Grammonota inornata*, showed strong preferences for the no-tillage habitat over the other three habitats. I hypothesize that these species must thrive in the thick herbaceous "straw-like" litter layer that is unique to this habitat. *Erigone autumnalis* was also trapped abundantly in this habitat and in the conventional-tillage field.

It seems at first surprising that species would "prefer" the no-tillage habitat to the extent of being much more rarely trapped in both the conventional tillage and the meadow habitats. However, Mangan & Byers (1989) showed that many old-field species remain during the establishment of no-tillage agroecosystems from old field habitats. Possibly the "no-tillage" species are adapted to life in early successional habitats. It seems that the no-tillage habitat may be to some extent ecologically similar to an old-field system for many of these species.

*Conventional-tillage field species:* The tetragnathid *Glenognatha foxi* was trapped abundantly in both agricultural habitats but rarely caught in the other two habitats. It is the only abundant species which showed no "preference" for either of the two agricultural habitats. The horizontal orb webs spun by this species were found from about 0.5–3.0 cm above the ground or litter surface of both habitats (Draney pers. obs.); presumably it is de-



pendent on habitat characteristics other than the ground surface architecture. The species has been found in a variety of mostly open, generally xeric situations (Levi 1980), including meadows, old field, saltmarsh, short grass, and cornfields, which are quite similar to sorghum fields. Their considerable ballooning ability (Crosby & Bishop 1936, as *Mimognatha foxi* McCook) makes them potentially beneficial colonizers of agricultural fields.

Besides *G. foxi* and *Erigone autumnalis*, four species were also characteristic of the conventional tillage agricultural field: *Pardosa atlantica*, *P. milvina*, and the linyphiids *Tennesseelum formicum* and *Eperigone fra-deorum*. *P. atlantica* was found in lower but considerable numbers in the no-tillage field and even in the grassy field border, whereas *P. milvina* was more restricted to the conventional tillage field.

**Maintenance of biodiversity in agroecosystems.**—Although more intensive sampling will undoubtedly yield additional species, it is clear that the four-habitat agroecosystem at Horseshoe Bend harbors a high diversity of species, similar in structure to that documented across an array of successional habitats elsewhere on the Piedmont Plateau (Berry 1966). Much higher species richness can be maintained in agroecosystems composed of a mosaic of habitats under different management regimes, as is the case at Horseshoe Bend, than in agroecosystems maintained as conventional monocultural landscapes. This is corroborated by the fact that Bailey & Chada (1968) trapped only 64 species from pitfalls in grain sorghum fields, compared with 112 species I trapped in the more complex sorghum/meadow/forest landscape at Horseshoe Bend. Habitat use patterns of individual spider species illustrate two mechanisms which may explain how landscape complexity results in higher spider diversity. First, many species seem to “specialize” in one or a few habitat types; populations may not be able to persist without these habitats. Thus, increasing the number of different habitat types will obviously increase the site-wide richness (gamma diversity) of the agroecosystem as a whole. Second, individuals are often found in habitats other than those in which the species is most abundant. Presumably these species often simply “spill over” to adjacent habitats during foraging and mate-searching behavior from

habitats where they are common. This results in higher species richness in each individual habitat (higher alpha diversity) via “mass effect” (Shmida & Wilson 1985). Diffusion of species into suboptimal habitats means these habitats may sometimes serve as refugia (*sensu* Duelli 1980), allowing species to persist in an ecosystem when their optimal habitat is disturbed by management practices. One practical effect of this is that species utilizing refugia may more rapidly recolonize their primary habitats after the disturbance (plowing, spraying, harvesting, etc.) subsides than would be the case if recolonization were solely by long-distance ballooning.

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## EFFECTS OF PREY SUPPLEMENTATION ON SURVIVAL AND WEB SITE TENACITY OF *ARGIOPE TRIFASCIATA* (ARANEAE, ARANEIDAE): A FIELD EXPERIMENT

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**ABSTRACT.** The effects of prey capture on web site tenacity and survivorship of *Argiope trifasciata* (Araneae, Araneidae) were studied in two old field habitats in southwestern Ohio. Adult females were studied in habitats dominated by grass or thistle plants. In manipulation plots, we added two crickets to the webs of approximately half the spiders. We were able to quantify differences in prey intake using morphological measurements that changed with food consumption. The spiders that did not receive supplemental food were similar in size to unmanipulated spiders in other areas that we censused. No differences were observed in survivorship or web site tenacity of spiders in grass vs. thistle habitats. No difference in survivorship was observed between fed spiders and those left to natural prey capture. However, spiders receiving supplemental prey relocated their webs less frequently than those spiders that were unsupplemented.

The selection of a site in which to live and forage can be a critical decision for a spider since food intake can have a substantial effect on the spider's ability to survive, grow, and ultimately reproduce (Riechert & Gillespie 1986; Vollrath 1987). The webs that spiders use as foraging tools are energetically costly (Prestwich 1977; Peakall & Witt 1976), and it is not possible for web-spiders to sample their habitat extensively before settling to forage in a particular place (Janetos 1986; Vollrath 1985, 1987). As a result, the initial selection of a site must be based on habitat features and the appropriateness of web attachment sites (Pasquet 1984; Hodge 1987a; Bradley 1993). Once the initial web is constructed, the spider acquires additional information on prey capture which can influence whether it stays or leaves.

A number of studies on a variety of species suggest that web-spiders use recent information on prey capture in deciding whether to stay or leave a particular site (Turnbull 1964; Janetos 1982; Olive 1982; Pasquet 1984; Vollrath 1985; Gillespie 1987; Rubenstein 1987; Hodge 1987b; Provencher & Riechert 1991; Bradley 1993). A variety of other factors unrelated to prey capture, such as the frequency of web destruction or damage, interactions

with conspecifics, the spider's age, and/or the action of predators, can influence a spider's decision to leave or remain in a given location (Eberhard 1971; Enders 1975, 1976, 1977; Wise 1975; Pasquet 1984; Spiller 1984; Vollrath & Houston 1986; Gillespie & Caraco 1987; Craig 1987; Smallwood 1993). Clearly, if a particular population is not food limited, prey capture should not have an effect on web site tenacity (Eberhard 1971; Enders 1976; Wise 1993). However, Olive (1981) argues that the phenologies of orb-weaving spiders, particularly those in the genus *Argiope* Audouin 1827, are tied to the seasonality of insects in their environment and that they evolved under the constraints of food limitation. In enclosure experiments with *Argiope trifasciata* (Forskål 1775), he found that they abandon sites with lower rates of prey capture and aggregate in areas where he supplied prey at a higher rate (Olive 1982). A field study with *A. keyserlingi* Karsch 1881, revealed that food supplementation, even over a few days, decreased the tendency of individuals to relocate their webs (Bradley 1993). However, in experiments with *A. aurantia* Lucas 1833, prey supplementation had no effect on web site tenacity; and the likelihood of wind damage appeared to be more critical to the web relocation decision (Enders 1975, 1976).

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Olive's (1981, 1982) results influenced us to further investigate the relationship between prey capture, survivorship, and web site tenacity in *A. trifasciata*. Since the abdomen of a spider expands as it feeds (Anderson 1974; Jakob et al. 1996), we were able to quantify differences between spiders that receive supplemental prey and those left to natural prey capture without disturbing them on their webs. In this way, we were able to verify that the spiders we fed consumed the prey we provided and experienced a change in their overall body condition in some significant way as a result of prey consumption. We then tested the hypothesis that prey supplementation would increase the survivorship and web site residence time of adult females in two structurally distinct habitats.

## METHODS

**Study species.**—*Argiope trifasciata* is a conspicuous orb-weaving spider found in gardens, tall weeds, and grasses in the eastern United States (Kaston 1948). Spiders emerge from egg sacs in May and June (Kaston 1948). Females mature in September when they are 15–25 mm in length, lay eggs in October and November, and die with the onset of winter (Scheffer 1905; Tolbert 1976). We selected this species for our investigation of the effects of prey capture on web relocation because: (1) their large size makes them easy to monitor in the field; (2) in 1993, the year before this study was conducted, we found them to be very abundant in old field habitats with densities as high as 0.82 spiders per m<sup>2</sup> (McNett 1995); and (3) although they rebuild the capture spiral of their web each day, they reuse the framework which attaches the web to the vegetation and, as a result, web relocation is costly in comparison to remaining at the same site (Enders 1976; Olive 1981).

**Study site.**—The study population inhabited old fields of the Miami University's Ecology Research Center, three miles north of Oxford, Butler County, Ohio, USA. Two manipulation plots (25 × 20 m) were established for prey experiments. One manipulation plot was set up in an area dominated by thistle (*Cirsium arvense*) and the second in an area dominated by grasses (*Elymus* sp., *Festuca* sp. and *Phleum* sp.). These two habitat types were those that the spiders preferred in 1993 (McNett 1995). Three 5 × 5 m census plots

in thistle and three 5 × 5 m census plots in grass, located at least 100 m away from the manipulation plots, were used as control areas in which the spiders were counted and measured but not fed.

**Prey availability.**—Background prey availability was assessed in both the thistle and grass habitats using sticky traps. Each trap consisted of a 20 × 20 cm sheet of plastic to which a thin layer of Tangle Trap<sup>®</sup> (Tangle Foot, Grand Rapids, Michigan) was applied. Traps were suspended with string that was tied either to natural vegetation or, when necessary, to metal reinforcing rods (3.5 m in height). Trap height was randomly determined within the range of 15–92 cm. These values were selected because they corresponded to the range of heights at which webs were found in 1993 (McNett 1995). Trap orientation was determined by randomly selecting a compass direction. A total of nine 400 cm<sup>2</sup> traps were hung in each of the six census plots in the early morning of 6 October 1994 and left for 24 h. The arthropods collected were identified to order, counted and measured to the nearest 0.1 mm.

**Morphological changes in the laboratory.**—Twenty-two adult female *A. trifasciata* were collected and allowed to establish webs in acrylic plastic (Plexiglas<sup>®</sup>) cages measuring 45 × 45 × 7.5 cm in the laboratory. The total body length and abdomen width of all the spiders were measured after web construction. We selected these measures because it was possible to take them without disturbing the spider in its web. After measurement, nine spiders were fed one cricket (*Acheta domestica*; approximately 150 mg in weight). All of the spiders were then left for 24 h during which time each individual replaced its capture spiral once. At that time, all of the spiders were measured again to determine if morphological differences as a result of feeding would be detectable.

During the course of two years of study of this species we were able to obtain morphological measurements in the laboratory of six females before and after eggsac deposition. Spiders were measured and left for 24 h. At that time the egg sac was noted and the spider remeasured. None of these spiders were fed between measurements.

**Prey manipulation.**—On 26–27 September 1994, 80 adult female *A. trifasciata* were



collected from areas at least 100 m outside the plots and individually marked on their abdomens with non-toxic paint. Spiders were held in the laboratory at 15 °C in vials 1 cm in diameter which were not large enough to allow web construction and therefore minimized any changes in their condition or hunger level. On 28–29 September 1994, all naturally occurring *A. trifasciata* from each of the two 25 × 20 m manipulation plots were removed. In the early morning of 30 September 1994, we introduced 40 randomly-chosen marked spiders to each plot by placing them on vegetation approximately 2 m away from other individuals. The next day, we searched the plots and marked the location of each spider's web by tying flagging to the vegetation near the web. There was a low establishment rate of marked spiders, so all unmarked spiders that moved into the plots after that date were assigned to a treatment group and included in further data collection. In comprehensive surveys conducted in 1993, we discovered that individuals never moved more than two meters (McNett 1995), so we were confident in our ability to follow and monitor web site changes of unmarked spiders that moved into our manipulation plots.

Introduced as well as unmarked individuals that established in the manipulation plots, were assigned randomly to one of two treatments: one group received supplemental prey and the other group was left to natural prey capture. Supplemented spiders received two adult crickets (*Acheata domestica*; approximately 300 mg) every other day in addition to the prey they captured naturally. Spiders received supplemental prey until they could no longer be located, at which time they were presumed dead. A total of 26 spiders was monitored in the thistle plot, 12 of which were fed crickets, and 30 spiders were monitored in the grass plot, 14 of which were provided with crickets.

Spider location was monitored daily from 1 October until no spiders could be found on 27 October 1994. If a spider was not found where it had been the previous day, the surrounding 60 m<sup>2</sup> area was visually searched. We were able to identify unmarked individuals by a combination of web location and abdominal patterns. Since we never observed a spider move more than 2 m from a previous web site, this large search area eliminated the

likelihood that a spider would be falsely assumed dead. If we found the spider, we recorded its new location but, if we were unable to find it, we assumed it was dead.

We measured abdomen width and total body length of all spiders in the manipulation plots to the nearest 0.1 mm on 4, 8 and 16 census days after the prey supplementation commenced. On those same dates, we counted and measured all of the spiders in our six census plots.

**Statistical analysis.**—The number and size of insects captured on sticky traps in grass and thistle were compared with a one-way ANOVA. The change in body size of laboratory spiders was compared using the *t*-test. The number of spiders in grass and thistle census plots over the course of the study were compared using a repeated measures ANOVA. We compared the abdomen width and body length of field measured spiders in three treatments (supplemented, unsupplemented and censored) in two habitat types (grass and thistle) using an two-way factorial ANOVA and then differences among the specific treatments were compared using Fisher Pairwise Comparisons. These three groups were compared 4, 8, and 16 census days after the prey supplementation was begun. Fed spiders on day 4 would have received prey twice (a total of four crickets), on day 8 they would have received prey four times (eight crickets), and on day 16 they would have received prey eight times (16 crickets).

In order to determine the impact of supplemental prey on survivorship, the total number of days over which we were able to locate fed and unfed spiders in the two habitats was compared using a two-way factorial ANOVA. In order to determine the impact of prey supplementation on web relocations, we also used the two-way factorial ANOVA to compare the movement frequency of fed and unfed spiders in the grass and thistle habitats.

## RESULTS

**Spider abundances.**—There was no difference between the number of spiders inhabiting thistle or grass in the census plots (Repeated measure ANOVA,  $F = 1.2$ ,  $P = 0.3$ ) (Table 1). Census plots had more spiders than we were able to establish in our manipulation plots ( $F = 18.96$ ,  $P = 0.032$ ) (Table 1). Since densities in manipulation plots were low com-



Table 1.—Number of spiders (mean  $\pm$  standard error) per square meter in old field habitats dominated by grass or thistle. In a two-way ANOVA, there were no differences between densities in grass and thistle habitats ( $F = 1.2$ ,  $P = 0.3$ ) but densities in manipulation plots were significantly lower than densities in census plots ( $F = 18.9$ ,  $P = 0.03$ ).

Plot type	Grass	Thistle
Census	0.52 $\pm$ 0.25	0.39 $\pm$ 0.12
Manipulation	0.06 $\pm$ 0.02	0.05 $\pm$ 0.02

pared to natural densities, we believe we successfully eliminated density as a potentially confounding factor in our study of the effects of habitat type and prey capture on web relocation.

**Prey abundance.**—Sticky traps in grass captured  $60.0 \pm 10.1$  insects in 24 h which was not significantly different from  $80.7 \pm 20.2$  insects captured by these traps in thistle (One-way ANOVA,  $F = 0.21$ ,  $P = 0.4$ ). The mean size of the insects captured by sticky traps in grass ( $2.39 \pm 0.19$  mm) was also very similar to the mean size captured in thistle ( $2.46 \pm 0.22$ ) ( $F = 0.07$ ,  $P = 0.7$ ). The insect orders Diptera and Hymenoptera made up more than 90% of the captures in both habitats.

**Morphological changes.**—In the laboratory, the consumption of one cricket was enough to increase total body length by  $0.42 \pm 0.16$  mm, whereas unfed individuals shrank by  $0.21 \pm 0.16$  mm in 24 h ( $t = 7.35$ ,  $P = 0.0005$ ) (Table 2). Likewise, the abdomen width of fed spiders increased by  $1.34 \pm 0.11$  mm while the abdomen width of unfed individuals decreased by  $0.22 \pm 0.15$  mm in 24 h ( $t = 60.70$ ,  $P < 0.0001$ ) (Table 2). These differences verify that these measurements are an indicator of recent feeding history and spider condition. The deposition of an eggsac re-

duced both spider abdomen width ( $t = 8.2$ ,  $P = 0.0004$ ) and total body length ( $t = 7.9$ ;  $P = 0.0005$ ) in the laboratory (Table 2). In addition, the spider's abdomen appeared shrunk-en and wrinkled after eggs were laid.

**Prey manipulation.**—Although the spiders increased in size over the course of the experiment, there were no significant differences observed between spiders inhabiting grass or thistle in the amount that either total body length (Two-way factorial ANOVA,  $F = 1.34$ ,  $P = 0.26$ ) or abdomen width ( $F = 0.24$ ,  $P = 0.63$ ) changed during the course of the study (Table 3). Unsupplemented spiders within our manipulation plots were not different in either measure of size from the control spiders in the census plots 4, 8 and 16 days after the food supplementation was begun (Fisher pairwise comparisons,  $P > 0.05$ ) (Fig. 1). However, spiders that received supplemental prey had wider abdomens than spiders in the other two groups (unsupplemented and censused) on all three dates tested (Fisher pairwise comparisons,  $P < 0.05$ ) (Fig. 1). Likewise, spiders receiving additional prey were longer than unsupplemented spiders in manipulation plots on all of those same dates and were longer than undisturbed spiders in the census plots on day eight. (Fisher pairwise comparisons,  $P < 0.05$ ) (Fig. 1).

We were able to find fed spiders for  $13.6 \pm 1.4$  days which was not significantly different from the survival of  $11.5 \pm 1.4$  days we observed for unfed individuals (Two-way factorial ANOVA,  $F = 0.99$ ,  $P = 0.33$ ) (Table 3). We were also able to locate spiders in the thistle  $14.6 \pm 1.5$  days and in the grass  $10.7 \pm 1.2$  days, but this difference was not significant at the 0.05 level ( $F = 3.68$ ,  $P = 0.06$ ) (Table 3).

Fed individuals remained at web sites an average of  $12.5 \pm 1.4$  days which was signif-

Table 2.—Measurements (mm) of the total body length and abdomen width of female *Argiope trifasciata* in the laboratory (mean  $\pm$  standard error). Fed individuals received one cricket (150 mg) whereas unfed individuals and those that produced eggsacs received no food.

Status	n	First measurement		After 24 hours		Difference	
		Length	Width	Length	Width	Length	Width
Fed	9	14.1 $\pm$ 0.8	7.1 $\pm$ 0.5	14.5 $\pm$ 0.7	8.5 $\pm$ 0.5	+0.4 $\pm$ 0.2	+1.3 $\pm$ 0.1
Unfed	13	15.2 $\pm$ 0.5	7.8 $\pm$ 0.4	15.0 $\pm$ 0.6	7.6 $\pm$ 0.4	−0.2 $\pm$ 0.2	−0.2 $\pm$ 0.2
Produced eggsac	6	14.1 $\pm$ 0.8	7.4 $\pm$ 0.4	12.5 $\pm$ 0.4	5.8 $\pm$ 0.4	−1.6 $\pm$ 0.2	−1.5 $\pm$ 0.2

Table 3.—Results of prey manipulation experiment in which fed spiders in thistle and grass were compared to spiders left to natural prey capture. Morphological measurements (abdomen width and total length) represent the difference between the fourth day after prey supplementation began and the sixteenth day after supplementation began. Data are expressed as mean  $\pm$  standard error.

	Fed	Unfed	Treatment	Vegetation	Interaction
Change in abdomen width (mm) in 12 days	(n = 10)	(n = 10)	F = 3.61 P = 0.08	F = 0.24 P = 0.63	F = 1.04 P = 0.32
Grass (n = 7)	1.50 $\pm$ 0.03	1.15 $\pm$ 0.55			
Thistle (n = 13)	2.18 $\pm$ 0.46	0.94 $\pm$ 0.20			
Both habitats	1.80 $\pm$ 0.30	0.98 $\pm$ 0.18			
Change in body length (mm) in 12 days	(n = 10)	(n = 10)	F = 1.22 P = 0.28	F = 1.91 P = 0.19	F = 0.08 P = 0.78
Grass (n = 7)	0.64 $\pm$ 0.73	0.10 $\pm$ 0.50			
Thistle (n = 13)	2.06 $\pm$ 0.54	0.83 $\pm$ 0.45			
Both habitats	1.19 $\pm$ 0.45	0.68 $\pm$ 0.38			
Total days located	(n = 26)	(n = 30)	F = 0.99 P = 0.325	F = 3.68 P = 0.061	F = 1.71 P = 0.187
Grass (n = 30)	11.0 $\pm$ 1.8	6.8 $\pm$ 1.2			
Thistle (n = 26)	14.3 $\pm$ 2.3	10.8 $\pm$ 2.2			
Both habitats	13.1 $\pm$ 1.8	8.6 $\pm$ 1.6			
Web relocations per spider	(n = 26)	(n = 30)	F = 5.60 P = 0.022	F = 0.12 P = 0.750	F = 2.98 P = 0.09
Grass (n = 30)	0.3 $\pm$ 0.1	0.4 $\pm$ 0.2			
Thistle (n = 26)	0.0 $\pm$ 0.0	0.6 $\pm$ 0.2			
Both habitats	0.2 $\pm$ 0.1	0.5 $\pm$ 0.1			

icantly longer than the unfed spiders which remained only  $8.7 \pm 0.2$  days. This difference verifies that fed spiders had significantly fewer web relocations (Two-way factorial ANOVA,  $F = 6.99$ ,  $P = 0.011$ ) (Table 3). Spiders in the thistle relocated their webs with the same frequency as the spiders located in the grass ( $F = 0.0001$ ,  $P = 0.95$ ) (Table 3).

DISCUSSION

An increase in prey capture by adult female *Argiope trifasciata* influences the decision to relocate or continue foraging in the same web site. These data are consistent with the results of Olive's (1982) enclosure experiments in which *A. trifasciata* individuals tended to leave areas in enclosures where food was not provided and aggregate in regions where food was supplemented. The fact that we were able to quantify an increase in spider condition via morphological measurements verifies that the food we were providing was sufficient to affect the spiders and provides a close link to food as the mechanism causing the changes in

behavior we observed. The fact that we could take these hunger measurements in the field without disturbing the spider is a desirable feature of this system. Since we were able to demonstrate that there was no impact of habitat or manipulation on these measures, only the supplemental prey that we provided can account for the differences we observed. Numerous studies have associated prey capture with web site tenacity (Turnbull 1964; Janetos 1982; Olive 1982; Riechert & Gillespie 1986; Gillespie 1987; Vollrath 1987; Rubenstein 1987; Bradley 1993 and references therein) but the quantification of prey capture in the past has always been prey in the web rather than some measure of actual intake by the spider as we were able to accomplish. One possible confounding factor that might affect our morphological measurements would be the production of an eggsac which substantially reduces the spider's abdomen size and changes its appearance. However, we did not observe the same kind of emaciation after egg laying in individuals we were monitoring



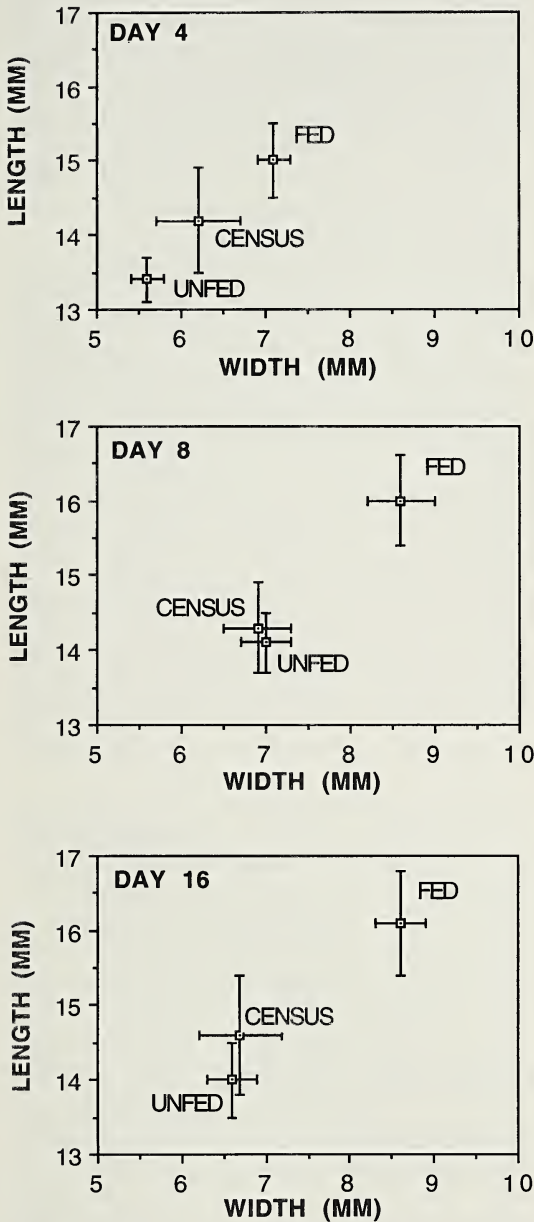


Figure 1.—Total body length and abdomen width (mean  $\pm$  SE) of spiders measured 4, 8 and 16 days after prey supplementation was begun. On Day 4, abdomen width was significantly different among groups ( $F = 4.43$ ,  $P = 0.003$ ) whereas total body length was not ( $F = 2.3$ ,  $P > 0.05$ ). On Day 8, both abdomen width ( $F = 3.95$ ,  $P = 0.007$ ) and total body length ( $F = 2.6$ ,  $P = 0.048$ ) were significantly different among the treatments. On Day 16, abdomen width was significantly different ( $F = 4.25$ ,  $P = 0.0085$ ) but total body length was not ( $F = 1.389$ ,  $P > 0.05$ ).

in the field that we saw in laboratory spiders. Since eggsacs are deposited very late in the season and since this species produces only one clutch per year (Tolbert 1976), it is likely that the spiders were dying shortly after the production of their egg sacs in the field, perhaps due to an increase vulnerability to predation or other environmental stressors. In any case, we would predict that the spiders receiving food supplements would be most likely to produce eggs since food intake is positively correlated with egg production in many species of spiders (Wise 1993 and reference therein). Therefore, if egg sac production were confounding our results, it would have reduced the likelihood of seeing the significant differences in body size we observed between the food supplemented and unsupplemented spiders in this study.

Spiders are frequently categorized as food limited in nature because they can survive long periods of starvation (Anderson 1970, 1974), have low metabolic rates (Anderson 1970; Carrel & Heathcote 1976; Nakamura 1987), and the fact that they tend to aggregate in high prey areas (Olive 1982; Rypstra 1989). It has been suggested that the plasticity of the abdomen in spiders is an adaptation to prey shortages because it enables spiders to consume large amounts of prey when it is abundant and store it for subsequent lean periods (Wilson 1971; Anderson 1974). Since the ability of a spider's abdomen to expand with consumption should decrease as it reaches its maximum, the substantial morphological changes we observed suggested that the spiders in our population were not close to satiation. Likewise the fact that manipulating the prey they consumed altered their web site tenacity provides further evidence that food is a limiting resource for this web-building spider (Wise 1993).

Food supplementation had more consistent effects on the spider's abdomen width than on total body length (Fig. 1). The abdomen is flexible and therefore changes size with feeding, whereas the cephalothorax is fixed in size for a given instar. Of our measurements, abdomen width is a more direct measurement of the changes in condition the spider experienced since any abdominal changes reflected in total body length are damped by the cephalothorax size, which cannot change. As a result, we saw less consistent differences among

treatments over the course of the experiment in body length than in abdomen width. In retrospect, a more accurate assessment of spider condition would have been obtained if we had taken measurements of the cephalothorax alone or some other body part that we knew did not change with feeding. Then we could have scaled body condition on absolute body size as recommended by Jakob et al. (1996).

Optimality theory predicts that the amount of time an organism remains at a site should be related to some combination of prey capture at that site and their investment in that site (Pyke et al. 1977). If this is true then, in a given habitat, spiders with more energetically costly webs should have longer web residence times since it should take them longer to recoup the investment in the web itself (Janetos 1986; Riechert & Gillespie 1986). The residence times that we recorded for unsupplemented *A. trifasciata* were around 8.5 days which is substantially longer than the time reported (3 days) for a wide variety of other orb-weaving spiders (Janetos 1982; Olive 1982; Riechert & Gillespie 1986; Smallwood 1993). Even the linyphiids with semi-permanent webs that Janetos (1982) studied had residence times around 5 days. In contrast, residence times of the linyphiid with a semi-permanent web, *Nerienne radiata* (Walckenaer 1844), were about 10 days; a value much closer to those we observed in *A. trifasciata* (Martyniuk 1983). Since *A. trifasciata* has a large web and reuses some portion of the support infrastructure, the construction of an entirely new web in a new location may be more costly than the other orb-weavers investigated. The large body size of this spider at late instars prevents from moving by ballooning and it appears to walk awkwardly off of the web. As a result, exploring for new web sites is a risky and energetically costly endeavor for *A. trifasciata*.

When spiders reach high densities then interactions with one another can influence web site tenacity (Hoffmaster 1986; Rypstra 1985; Smallwood 1993). It seems unlikely that web take-overs or spider interactions on the webs were factors in this study. In experimental plots the spider density was only 0.05 individuals per m<sup>2</sup> in the thistle and 0.06 individuals per m<sup>2</sup> in the grass and the spacing was fairly uniform across the plots. The low densities in these experiments and the fact that

we never observed individuals moving more than two m in a web relocation event (McNett 1995), suggest that intraspecific interactions were not very important in our these experiments. Additionally, it may be that the low densities with which we were working and the elimination of spider-spider interactions as a disturbance, accounts for the relatively long residence times that we observed compared to other orb-weaving spiders.

The size and web relocation behavior of *A. trifasciata* in the grass and thistle habitats we compared were surprisingly similar. Prey capture of spiders in thistle must have been similar to that in the grass because we uncovered no morphological differences in the spiders inhabiting the two habitats (Table 2). This result is supported by our captures in insect traps which failed to reveal any differences between these two habitats in prey activity at this time in the season. Since Enders (1975, 1976) related web relocation to destruction by wind, we expected to see more relocation events by spiders living in grass since it offers a less sturdy web support than thistle. Perhaps, at least in the season of this study, wind was not sufficiently damaging to affect the spider's behavior.

Although not significant at the 0.05 level, it is tempting to speculate on the nearly significant difference in survival between animals in the thistle and those in the grass ( $P = 0.06$ , Table 2). Indeed, since we were monitoring such a short period in the end of the spider's life, it is surprising that there is any suggestion of a difference by habitat in the timing of their death at the onset of winter. Horton (1980) found that *Argiope* in North American old field habitats are subject to substantial bird predation and that the zig-zag stabilamentum offers them some protection from birds. For those of us who have monitored spiders in thistle habitats, it is not difficult to believe that the irritating leaves of this plant could provide the spiders some protection from a variety of vertebrate predators which may have contributed to the near significant difference in survival we observed.

In summary, these data demonstrate that change in prey intake is a major factor influencing web site tenacity of these large orb-weaving spiders. The difference in body condition between spiders that received supplemental prey and those that did not was the



overriding difference between the spiders studied here even though we also compared spiders in two structurally different old field habitats. The ease with which we could verify changes in body condition make detailed analysis of the impact of food intake on the ecology and behavior of *A. trifasciata* in a natural setting possible.

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## PHYLOGENETIC ANALYSIS OF PISAURINE NURSERY WEB SPIDERS, WITH REVISIONS OF *TETRAGONOPHTHALMA* AND *PERENETHIS* (ARANEAE, LYCOSOIDEA, PISAURIDAE)

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**ABSTRACT.** Apomorphic characters of the Pisaurinae Simon 1898, here recognized as a monophyletic clade comprising 19 nominal pisaurid genera, are described. The genera *Perenethis* L. Koch 1878 and *Tetragonophthalma* Karsch 1878 are revised. Three Asian, two African and one Australian species of the genus *Perenethis* are recognized. The Asian species of the genus *Perenethis* comprise *Ocyala dentifasciata* O. Pickard-Cambridge 1885, *Tetragonophthalma fascigera* Bösenberg & Strand 1906, and *Tetragonophthalma sindica* Simon 1897. A lectotype is designated for the Australian species *Perenethis venusta* L. Koch 1878. *Perenethis parkinsoni* Dahl 1908 is regarded as a subjective junior synonym of *P. venusta*. The African species of *Perenethis* are *Tetragonophthalma simoni* Lessert 1916, and *Tetragonophthalma symmetrica* Lawrence 1927 with its subjective junior synonyms *Perenethis huberti* Blandin 1975, *Perenethis lejeuni* Blandin 1975 and *Pisaurellus badicus* Roewer 1961. A lectotype is here designated for the African species *Perenethis simoni*. *Phalaea vulpina* Simon 1898 is the only recognized species of the genus *Tetragonophthalma* with eight subjective junior synonyms: *Tetragonophthalma balsaci* Blandin 1976, *Phalaea crassa* Thorell 1899, *Phalaea ferox* Pocock 1899, *T. guentheri* Roewer 1955, *T. lecordieri* Blandin 1976, *T. pellengea* Roewer 1955, *Phalaea thomensis* Simon 1909, and *T. wittei* Roewer 1955. *Cispius novus* Caporiacco 1941 and *Cispius tertali* Caporiacco 1941 are both subjective junior synonyms of *Cispius aethiopicus* Caporiacco 1939, now placed in the genus *Charminus* (NEW COMBINATION). The genera *Charminus* Thorell 1899, *Cispius* Simon 1898, *Tetragonophthalma*, *Afropisaura* Blandin 1976, *Perenethis*, *Maypaci* Simon 1898, and *Polyboea* Thorell 1895 form a monophyletic group within the Pisaurinae, here called *Perenethis* genus group. The copulatory organs of this group are figured in detail, the vulval structures for the first time. Males and females of the poorly-known monotypic genus *Polyboea* are described, and their copulatory organs are figured for the first time. A cladistic analysis of the *Perenethis* genus group is presented. The Afro-Asian distribution of members of the clade *Polyboea* and *Maypaci* and the *Perenethis*-clade is hypothesized to be the result of independent range extensions during the expansion of suitable habitats between the Miocene and the beginning of the Pleistocene.

The nursery-web spiders (Family Pisauridae) currently contain 54 nominal genera (Platnick 1993), many of them only poorly known. Members of the family are distributed worldwide, displaying great variations in habitus, size and life style. Several genera contain large species (up to 30 mm body length) hunting on the surface of freshwater ponds and streams, (e.g., members of the worldwide genus *Dolomedes* Latreille 1804 and the African-Asian genus *Thalassius* Simon 1885 (see Sierwald 1987)), or hunt in trees like spiders of the African genus *Tetragonophthalma*. Other genera contain small spiders (body length 3–4 mm) hunting on permanent webs, (e.g., in the American genus *Architis* Simon 1898 (see Carico 1981)). Spiders of the name-

bearing Palearctic genus *Pisaura* Simon 1885 hunt in the vegetation. A well-known species is *Pisaura mirabilis* (Clerck 1757), famous for the male's nuptial gift presented to the female during courtship. Morphological data, especially of copulatory organs, life history data and revisionary work at the alpha-taxonomic level, are lacking for most Pisauridae. For many genera, only very few (type) specimens are cataloged and thus accessible in collections. Most American (Carico 1972–1981) and some African (Blandin 1974a–1979b; Sierwald 1987) pisaurid genera were revised recently.

The main systematic problem of this family concerns the delineation of the Pisauridae and the definition of subfamilies. No synapomor-

phies have been recognized to date that would distinguish at least the majority of pisaurid genera as a single clade. The often cited nursery-web appears not to be restricted to pisaurid genera, but similar (homologous?) webs are constructed by *Peucetia* Thorell 1869 (Family Oxyopidae; Brady 1964; Zahl 1971, color photo of *Peucetia* nursery-web) and *Ancylometes* Bertkau 1880 (see Merrett 1988). The systematic position of the latter is uncertain, as it shares characters with members of the family Ctenidae (eye pattern, reduced third claw), a group that is presumably not monophyletic (Griswold 1993; Huber et al. 1993). Eye arrangements have a long tradition in identification, separation and delimitation of spider taxa at and below the family level. However, the general "pisaurid" pattern (recurved posterior eye row wider than anterior eye row) occurs also at least in the families Trechaleidae, Lycosidae, Psecridae, Ctenidae, Acanthoctenidae, and Senoculidae. Formerly, the pisaurid genera were grouped in the three subfamilies Pisaurinae, Thaumasiinae and Thalassinae (Simon 1898a; Roewer 1954). Lehtinen's (1967) suggested placement of "pisaurid" genera in different families (Dolomedidae = Thaumasiinae and Pisauridae = Pisaurinae) and superfamilies (Lycosoidea and Pisauroidae) was poorly substantiated, the argumentation lacking supportive evidence in form of clearly defined synapomorphies (Brignoli 1983; Sierwald 1990). New catalogs (Platnick 1989, 1993) listed pisaurid genera without reference to subfamilies.

Recent progress in systematic studies identified 10 genera, originally assigned to Pisaurinae and Thaumasiinae, as a monophyletic clade. Based in part on characters of the eye arrangement and synapomorphies in male and female copulatory organs (Sierwald 1993), these 10 genera were placed in the re-erected South American family Trechaleidae Simon 1890 (Carico 1986, 1993). The present study describes the defining characters of a monophyletic clade consisting of 18 pisaurid genera all related to the genus *Pisaura* and for which Simon's name Pisaurinae is available (Tables 2, 3). This study also presents a cladistic analysis of a monophyletic clade within the here redefined Pisaurinae, the *Perenethis* genus group. This group contains the genera *Charminus* Thorell 1899, *Cispus* Simon 1898, *Af-*

*ropisaura* Blandin 1976, *Tetragonophthalma* Karsch 1878, *Perenethis* L. Koch 1878, *Maypaci* Simon 1898 and *Polyboea* Thorell 1895. The majority of characters used in the cladistic analysis stem from the copulatory organs and the internal female organs for these taxa are figured for the first time. Taxonomic revisions of the genera *Tetragonophthalma* and *Perenethis* are included. The distribution of members of the *Perenethis* genus group is noteworthy and discussed below. *Charminus*, *Cispus*, *Afropisaura*, *Tetragonophthalma* and *Maypaci* are restricted to Africa, the monotypic genus *Polyboea* to Asia, and the genus *Perenethis* is widely distributed in Africa, Asia, and Australia. The African-Asian distribution pattern observed in this group of taxa occurs in other pisaurid and non-pisaurid spider groups as well. The cladogram obtained through the phylogenetic analysis suggests hypotheses regarding the origin of this distribution pattern.

## METHODS

Specimens were made available by the institutions and their curators listed in the Acknowledgments. The institutional acronyms were taken from Arnett et al. (1993). Specimens designated and published as allotypes by original authors are in fact paratypes, specimens designated as néallotypes in subsequent publications have no validity under ICZN regulations (ICZN 1985).

**Phylogenetic analysis of the *Perenethis* genus group.**—*Outgroup:* The African pisaurid genera *Charminus* and *Cispus*, themselves sister taxa, serve as out-groups in the cladistic analysis. The membranous, sac-like anterior section of the female copulatory duct as it occurs in *Charminus camerunensis* Thorell 1899 (Fig. 5) and in all genera of the ingroup is the synapomorphy for ingroup and outgroup. The sister-group relationship of *Charminus* and *Cispus* is in this data set supported by one synapomorphy, the procurved ridge (= carina) of the epigynum (Figs. 4, 6). *Characters:* Character scoring is presented in Table 4. The character matrix contains 35 characters (17 binary, 18 multistate) with 98 states: 17 characters with 45 states from male copulatory organs, 11 characters with 31 states from female copulatory organs, and 7 somatic characters with 22 states. An artificial amalgam taxon of the genus *Cispus*, combin-



ing the female characters from *Cispium variegatus* Simon 1898 (type species of the genus, male unknown) and the male characters of *Cispium thorelli* Blandin 1978 (female unknown) was used in the data matrix. This procedure became necessary due to the scarcity of males in identified museum collections. The copulatory organs of *Cispium maruanus* (Roewer 1955), the only species for which both sexes are known, are similar to *variegatus* and *thorelli* respectively (Blandin 1978a, figs. 8, 19; only a single male specimen, the paratype, of *maruanus* is known). **Tree generation:** Trees were generated with the software package Hennig86, version 1.5 (Farris 1988), using the "ie\*" command (implicit enumeration, calculates all possible shortest trees). All multistate characters were treated unordered (non-additive, implemented with the "ccode-;" command). **Character optimization:** Characters were optimized on the trees using CLADOS, version 1.2 (Nixon 1992), which permits comparing ACCTRAN and DELTRAN optimization (implemented in "Un Equis" Mode, using the commands "o" [ACCTRAN] and "CTL o" [DELTRAN]). Figure 2 shows the ACCTRAN optimization of characters, and Table 5 notes the characters that differ under DELTRAN optimization. Characters were mapped on the cladogram shown in Fig. 2 using the HOM = 0 (default) settings: Only those character state changes are indicated as homoplastic (white rectangles) that designate more than one independent origin of that state within this data set. Non-homoplastic character state changes are indicated as black rectangles.

**Usage of terms.**—**Character:** The term refers to an actual structure (e.g., conductor). Identical terms used for particular structures in male and female copulatory organs imply homology. A particular structure may appear in several different conditions (= character states). Morphologically indistinguishable character states were given identical codes in the data matrix, without *a priori* regard for the distribution of that particular state within the 14 species. To facilitate precise comparison of positions of various elements in the male genital bulb, the terms "proximal" and "distal" were used as defined below. **Male palpal organs:** Differing from common usage, the terms "proximal" and "distal" on the tegulum of the male palp refer to the position of a

particular part in relation to the trajectory of the sperm duct. In all Pisauridae studied so far, the reservoir of the sperm duct forms a single spiral within the tegulum (Sierwald 1990, fig. 2). Following the course of the sperm duct, starting at the fundus in the subtegulum, apophyses inserting on the tegulum near the fundus are considered proximally located. Apophyses inserting closer to the ejaculatory duct, i.e., the embolic base, are referred to as being distal. Often these topological data can only be assessed in the expanded bulb. The terms dorsal, ventral, basal, apical, retrolateral, and prolateral are used descriptively for positions within the unexpanded bulb in ventral view. Dorsal and ventral refer to the position of a particular part being within the depth of the unexpanded genital bulb. Ventrally located parts are mostly visible in the unexpanded bulb in ventral view (as figured here). **Female copulatory organ:** The term epigynum refers to the external parts, the term vulva to the internal parts of the female copulatory organ. Copulatory duct describes that part of the duct that connects the copulatory opening with the spermatheca. Fertilization duct defines that part of the duct that connects the base of the spermatheca with the uterus externus. The spermatheca in Pisauridae consists of a rounded head, bearing pores, attached to the stalk of the spermatheca. The stalk of the spermatheca, containing the spermathecal duct, connects to the base of the spermatheca (Fig. 1b).

**Dissections, measurements, drawings.**—Dissections and drawings follow the procedure described in Sierwald 1989b, 1990. All measurements for body length, prosoma length and width and leg length are in mm. Recorded leg length in species descriptions is given for leg I. Leg segments were measured dorsally. Relative spine length is compared between taxa. The tibial spines are rather uniform in length on all legs of an individual and similar in length to most metatarsal and femoral spines (spines notated as "1" in Table 6), except when noted otherwise (spines notated as "i" or "I" in Table 6). To assess relative spine length a ratio was calculated by dividing the absolute length of one spine of the second pair of ventral spines of tibia I by the width of tibia I. The calculation was repeated for up to five individuals if available. A ratio of three indicates the spine being 3× as long as the





Table 1.—Abbreviations on figures and in text.

Copulatory organs	
A	sclerite A at base of embolic division (♂)
bh	basal hematodocha (♂)
bmt	basal membranous tube (embolic division, ♂)
bs	base of spermatheca (♀)
c	conductor (♂)
ca	carina of epigynum (♀)
cd	copulatory duct (♀)
co	copulatory opening (♀)
db	dorsal branch of <i>dt</i> a (♂)
ds	spermathecal duct (♀)
dst	distal sclerotized tube (embolic division, ♂)
dta	distal tegular apophysis (♂)
dtp	distal tegular projection (♂)
e	embolus (♂)
epf	epigynal folds (♀)
fd	fertilization duct (♀)
fo	fossae, epigynal pits on carina (♀)
hs	head of spermatheca (♀)
ll	lateral lobes of epigynum (♀)
lf	lateral flap at conductor
ma	median apophysis (♂)
mf	middle field between <i>ll</i> (♀)
p	petiolus (♂)
pp	pars pendula of embolus (♂)
rta	retrolateral tibial apophysis (♂)
ss	stalk of the spermatheca (♀)
st	subtegulum (♂)
t	tegulum (♂)
tr	truncus of embolus (♂)
vb	ventral branch of <i>dt</i> p (♂)
vta	ventral tibial apophysis (♂)
Legs	
Fe	femur
Pa	patella
Ti	tibia
Me	metatarsus
MeTa	metatarsus-tarsus
PaTi	patella-tibia
Eyes	
AE	anterior eyes
AER	anterior eye row
ALE	anterior lateral eyes
AME	anterior median eyes
PE	posterior eyes
PER	posterior eye row
PLE	posterior lateral eyes
PME	posterior median eyes
Miscellaneous	
ch	character, see Table 4

longitudinal stripes, rows of dark brown-to-black hairs often contrasting with the bright stripes. These color pattern elements occur also outside the Pisaurinae within the Pisauridae *sensu lato*, e.g., in *Dolomedes*. Leg spination (Table 6): Spination pattern uniform on certain leg segments throughout the Pisauridae *sensu lato* (e.g., Fe II, III), others show several, often genus-typical character states (e.g., patellar spination; see below in description of genera). Spine-length ratio: Small, thin-legged, web-living Pisauridae (e.g., *Polyboea*) with longer spines than medium-sized species hunting in vegetation (e.g., *Charminus*, *Pisaura*); short spines predominantly in large-sized species (e.g., *Maypaci*us and *Tetragonophthalma*) (see Methods for calculation of ratio).

Female copulatory organ: (Figs. 1a,b). As in other Lycosoidea, the female copulatory organ consists of two lateral longitudinal folds, the epigynal folds (Sierwald 1989b). The internal pouches of these folds each contribute a copulatory duct, a spermatheca and a fertilization duct to the vulva. In the Pisaurinae, the epigynal folds run longitudinally, diverging (e.g., *Perenethis*) or converging anteriorly (e.g., *Charminus*) or forming curves (e.g., *Pisaura*). The copulatory opening is situated along the anterior section of the folds, thus the trajectory of the anterior section of the epigynal folds determines the position of the copulatory openings relative to other features within the female organs and the course of the anterior part of the copulatory duct in the vulva, e.g., whether it starts medially or laterally. In the genera *Afropisaura*, *Tetragonophthalma*, *Perenethis*, *Maypaci*us, and to a lesser degree, *Polyboea*, the epigynal folds diverge strongly anteriorly, thus placing the copulatory openings laterally. Epigynum: The integument between (middle field, *mf*) and around the folds (lateral lobes, *ll*) is often strongly sclerotized and may form projections, grooves, pits, hoods, ridges, etc. When comparing the genera *Pisaura* and *Afropisaura*, Blandin (1976b) suggested interesting homology-hypotheses concerning the transverse ridge and the two pits (Fig. 1a). These elements can be identified in the epigyna of all 18 pisaurine genera. The integument anterior to the epigynal folds forms a transverse ridge (carina, *ca*) that can be straight, procurved or recurved, forming a large sclerotized lip, can be entire or separated in two branches. The

Table 2.—Variable characters in the Pisaurinae. <sup>1</sup> Originally described by Simon (1898a: 295) as *Caripeta* (name preoccupied), *Caripetella* nom. nov. by Strand (1928). <sup>2</sup> Data from Blandin 1979a. <sup>3</sup> Considered a synonym of *Nilus* by Simon (1889a: 296). ♂ males only known, ♀ females only known. Character states in parentheses ( ) refer to a variation occurring in few individuals within a species. Character states in brackets [ ] refer to a variation in a single species of the genus. Strongly procurved anterior eyes occur in distinctly different states (states: procurved I through IV) in the pisaurine genera.

	PME-Size	ALE-Size	AER-Shape	Chelicerai teeth	
				Number	Size
<i>Afropisaura</i> Blandin 1976	PME>AME	ALE≥AME	proc/straight	3	equal
<sup>2</sup> <i>Caripetella</i> Strand 1928 <sup>1</sup>	PME>AME	ALE>AME	procurved	4	equal
<i>Charminus</i> Thorell 1899	PME>AME	ALE=AME	recurved	3 (4)	unequal [equal]
<i>Chiasmopes</i> Pavesi 1883	PME>AME	ALE>AME	procurved III	3	equal
<i>Cispius</i> Simon 1898	PME>AME	ALE<AME	recurved (straight)	3 [2]	unequal
<sup>2</sup> <i>Cladynis</i> Simon 1898 <sup>2</sup>	PME>AME	ALE<AME	recurved	3	unequal
<i>Dendrolycosa</i> Doleschall 1859	PME>AME	ALE>AME	recurved	3	unequal
<i>Euprosthenops</i> Pocock 1897	PME>AME	ALE>AME	procurved IV	3 (4)	equal
<i>Euprosthenopsis</i> Blandin 1974	PME>AME	ALE>AME	procurved IV	3	equal
<i>Maypactus</i> Simon 1898	PME<AME	ALE<AME	procurved II	2	equal
<sup>2</sup> <i>Paracladynis</i> Blandin 1976	PME>AME	ALE>AME	recurved	3	equal
<i>Perenethis</i> L. Koch 1878	PME>AME	ALE<AME	procurved	2	unequal
<i>Pisaura</i> Simon 1885	PME>AME	ALE>AME	straight	3	unequal
<i>Polyboea</i> Thorell 1895	PME>AME	ALE>AME	procurved	2	equal
<i>Rothus</i> Simon 1898	PME>AME	ALE>AME	procurved	2	equal
<sup>2</sup> <i>Tallonia</i> Simon 1889 <sup>3</sup>	PME=AME	ALE=AME	recurved	3	equal
<i>Tetragonophthalma</i> Karsch 1878	PME>AME	ALE>AME	procurved I	3	equal
<sup>2</sup> <i>Thalassiopis</i> Roewer 1955	PME>AME	ALE>AME	recurved	4	equal
<i>Vuattouxia</i> Blandin 1979	PME>AME	ALE>AME	procurved	3	equal



Table 3.—Systematic position of genera listed previously in the Pisaurinae by Simon (1898:282–297) and Roewer (1954:110–126). <sup>1</sup> Type species congeneric with *Dolomedes* based on description in Roewer (1955:190, figs. 73a, b). Also discussed by Blandin (1978:38). <sup>2</sup> Listed in Simon’s Supplément Générale (1898:1045) and assigned to the Dolomedae. <sup>3</sup> Specimens examined for this study. <sup>4</sup> Listed in the Supplément Générale (1898:1044) and assigned to Pisaureae.

Simon 1898	Roewer 1954	Current systematic position
<i>Architis</i> Simon 1898	<i>Architis</i> <i>Cispiolus</i> Roewer 1955 <i>Cispiomma</i> Roewer 1955	Pisauridae sensu lato synonym of <i>Dolomedes</i> <sup>1</sup> synonym of <i>Cispilus</i> (by Blandin 1978a:44)
	<i>Enna</i> Cambridge 1897 <sup>2</sup>	transferred to Trechaleidae (by Carico 1986)
	<i>Euprosthennomma</i> Roewer 1955	synonym of <i>Euprosthenops</i> (by Blandin 1976:67)
<i>Eurychoera</i> Thorell 1897	<i>Eurychoera</i>	Pisauridae sensu lato <sup>3</sup>
<i>Ischalea</i> L. Koch 1872	<i>Ischalea</i> <i>Melocosa</i> Gertsch 1937 <i>Pelopatis</i> Bishop 1924	transferred to Stiphidiidae transferred to Lycosidae Synonym of <i>Pisaurina</i> (by Carico 1972:297)
<i>Phalaea</i> Simon 1898	synonym of <i>Tetragonophthalma</i>	
<i>Pisaurina</i> Simon 1898	<i>Pisaurina</i>	Pisauridae sensu lato
<i>Sisenna</i> Simon 1898	<i>Sisenna</i>	transferred to Trechaleidae (by Sierwald 1990:51)
<i>Spencerella</i> Pocock 1898 <sup>4</sup>	<i>Spencerella</i>	synonym of <i>Chiasmopes</i> (by Blandin 1974a:311)
<i>Staberius</i> Simon 1898	<i>Staberius</i>	Pisauridae sensu lato
<i>Thanatidius</i> Simon 1898	<i>Thanatidius</i>	synonym of <i>Pisaurina</i> (by Carico 1972:297)
Genera of currently unknown affinities		
	<i>Cispinilus</i> Roewer 1955	no specimens examined
<i>Nilus</i> O.P.—Cambridge 1876	<i>Nilus</i> <i>Phalaeops</i> Roewer 1955	no specimens examined no specimens examined
<i>Stoliczka</i> O.P.—Cambridge 1885	<i>Stoliczka</i>	no specimens examined

carina possesses two lateral pits here termed fossae (*fo*). The fossae may be located directly above the copulatory openings, lateral to them or between them. Their positional relationship to the copulatory opening and additional depressions (e.g., as in *Afropisaura*) probably determine the fixation mechanism needed to securely connect the expanded male bulb and the epigynum. Thus, the Pisaurinae invite the study of copulation mechanics and its evolutionary change. Vulva: The slitlike copulatory openings lead into the mostly membranous, saccate copulatory ducts, often forming loops. In the genera *Afropisaura*, *Tetragonophthalma*, *Perenethis*, and *Polyboea* the copulatory duct possesses two large saccate loops, with the first loop running from the lateral copulatory opening towards the middle of the vulva. The copulatory ducts (*cd*) enter the stalk (*ss*) of the laterally located spermatheca close

to the perforated spermathecal heads (*hs*). The coiled spermathecal ducts (*ds*) enter the large base of the spermatheca (*bs*), which contains either an enlarged lumen or additional coils of the duct. The coiling pattern of the spermathecal duct is often species-specific. The fertilization duct (*fd*) is short and sclerotized, originating at the medial portion of the spermathecal base. Such tri-partite spermatheca, consisting of head, stalk and base, has been found in many genera of Lycosoidea (Järvi 1905; Sierwald 1989b, Griswold 1993) and other members of the RTA-Clade (which comprises all families in which males possess a retrolateral tibial apophysis; Coddington & Levi 1991).

Male copulatory organ: The male copulatory organ of *Pisaura* has been described and figured in detail elsewhere (Sierwald 1990). The most conspicuous feature is the presence

of three apophyses, the conductor (*co*) on the retrolateral side, the median apophysis (*ma*) and distal tegular apophysis (*dta*) ventrally in the center of the unexpanded bulb (Fig. 1c). The distal tegular apophysis represents a conspicuous synapomorphy for the Pisaurinae. The distal tegular apophysis was labelled fulcrum by Blandin (1976b) but is not homologous with the "fulcrum" *sensu* Comstock (1910) in *Dolomedes* (Sierwald 1990). In contrast to other pisaurid genera, members of the Pisaurinae possess a simple retrolateral tibial apophysis (*rta*) with a single rounded or pointed tip. A petiolus is well developed. The tegulum is bowl-like, with the sperm duct following the outer margin of the bowl. The upper surface of the tegulum is partly sclerotized but membranous around the base of the median apophysis and around the ventral branch of the distal tegular apophysis, permitting both to tilt out of their position during inflation. The distal tegular projection (*dtp*) is broadened and sclerotized, some with one or two humps. The base of the distal sclerotized tube of the embolic division appears to be supported by the sclerotized humps of the distal tegular projection during expansion of the bulb (Fig. 11).

The conductor (*co*), an outgrowth of the retrolateral tegular wall, displays several genus-typical character states within the Pisaurinae. An often strongly-sclerotized outer retrolateral wall and a more or less membranous inner prolateral wall that is partly inflatable are the basic components. The inner wall may feature membranous folds, along which the embolus rests in the unexpanded bulb (Figs. 8, 10). The conductor is a very important feature for the analysis of the Pisaurinae, since various parts of the conductor display several states (see under Character description below). The slender median apophysis (*ma*) is shorter than the distal tegular apophysis, with a sclerotized pointed tip often forming a hook. Its basal and prolateral sections are membranous and expandable. The large distal tegular apophysis (*dta*) has a dorsal (*db*) and a ventral branch (*vb*). The ventral branch anchors the distal apophysis in the tegulum, the dorsal branch connects to the basal membranous tube (*bmt*) of the embolic division. The shape of the ventral branch resembles a scapula and may carry a wing-shaped flap apically (Figs. 54, 57, 64). The ventral and dorsal branches are joined

apically, forming a hook-shaped beak pointing retrolaterally. Next to the dorsal branch, within the basal membranous tube of the embolic division lies a sclerite labelled "A" in Figs. 11, 14, 29, 94, 96, 99. The sclerite is present in *Pisaura* (see Sierwald 1990, fig. 45, not labelled). In most species sclerite A is visible only in expanded palps. The embolic division, connected to the distal tegular projection via a membranous tube (basal membranous tube, *bmt*), consists of the distal sclerotized tube (*dst*), fused to the truncus of the embolus, and the pars pendula (*pp*). The embolus is of varying length and often whiplike.

**Natural history.**—Data on behavior and life history are scarce. Apparently, the majority of pisaurine spiders hunt in the vegetation. Members of a few genera, *Euprosthenops* Pocock 1897 (see Gerhardt & Kästner 1938) and *Polyboea* (see Koh 1989) build webs for prey capture. Very young *Pisaura mirabilis* hunt in webs (Lenler-Eriksen 1969); their webs resemble those built by young *Dolomedes* and young *Pisaurina* Simon 1898, and the permanent webs built by *Architis* (see Carico 1985; Nentwig 1985; Sierwald 1990). The copulatory behavior of *Pisaura mirabilis* is well known: The male presents a wrapped prey item to the female (Hasselt 1884; Britton 1958; Nitzsche 1988). Unfortunately, the copulatory behavior of other pisaurine species is unknown. Nursery-webs have been reported from *Pisaura mirabilis*, *Afropisaura* and other pisaurid genera outside the Pisaurinae (Sierwald 1990).

**Specimens examined.**—Members of the genera *Afropisaura*, *Charminus*, *Cispius*, *Maypaci*, *Perenethis*, *Polyboea*, and *Tetragonophthalma* examined for this study are listed below under the description of each genus. Other material: *Caripetella madagascariensis* (Lenz 1886): **MADAGASCAR:** Fianarantsoa Province, P.N. Ranomafana, Talatakelly, 21°15'S, 47°25'E, 900 m, 1♀, 5–7 October 1993 (Scharff, Larcher, Griswold, Andriamasimanana) (currently CASC). Toamasina Province, P.N. Perinet, 1000 m, near Andasibe, 18°56'S, 48°24'E, 2♀, 4–5 November 1993 (Coddington, Larcher, Griswold, Andriamasimanana, Scharff) (currently CASC). Antsiranana Province, Marojejy Reserve, 8.4 km NNW Manantenina, 14°25'S, 49°45'E, 700 m, numerous ♂♀, 10–16 November 1993 (currently CASC). *Chiasmopes namaquensis* (Roewer 1955): **SOUTH AFRICA:** Cape Province, Die-Vlug, near Avontuur, fynbos dung trap, 1♀, 16–19 December 1981 (S. & J. Peck) (AMNH). *Chias-*



*mopes* sp.: **SOUTH AFRICA**: Natal, Cathedral Peak Forest, 75 km WSW of Estcourt, grassland, pan trap, 2♂, 13–31 December 1979 (S. & J. Peck) (AMNH). *C. hystrix* (Berland 1922): **SOUTH AFRICA**: Transvaal, Ohrigstad, 14 km S Belfast, 1♀, 27–29 December 1990 (V.D. & B. Roth) (CASC). *Dendrolycosa* sp.: **PHILIPPINES**: Luzon, Ilocos Norte, Pagudpud, Subec, 1♂, 23 May 1987 (C.K. Starr) (USNM). **MALAYSIA**: Perak, Cameron Highlands, 1♀ (Koh 84.06.12.10). *Pahang*, Fraser's Hill, 1♀ (Koh 76.11.16.08). **BRUNEI**: 1♀ with egg sac, (Koh 83.01.26.02). **PAPUA NEW GUINEA**: Madang Province, Nobonob Hill, 7 km NW Madang, 5°10'S, 145°5'E, 2♂, 1 May 1988 (W.J. Pulaski) (CASC). *Euprostenops australis* Simon 1898: **TANZANIA**: Inside W. slope Ngorongoro Crater, 1850 m, 1♀, 21 October 1957 (E.S. Ross & R.E. Leech) (CASC). *Seronera*, Serengeti National Park, 1450 m, 1♀, 24 November 1967 (E.S. Ross & A.R. Stephen) (CASC). *Euprostenops bayaonianus* (Capello 1866): **ZIMBABWE**: Kariba, 2♂, 16 August 1990 (V.D. & B. Roth) (CASC). **ZAIRE**: Faradje III. Lessert det., 1♀ (AMNH). *Euprostenops biguttatus* Roewer 1955: **ZIMBABWE**: Mazabuka, Matthyse leg., 1♂, 17 September 1952 (AMNH). **ANGOLA**: Lunda Province, Nova Chavez, 1♀, 14–16 September 1949 (B. Malkin) (CASC). *Euprostenopsis* sp.: **SOUTH AFRICA**: Transvaal, Klaserie, Guernsey Farm, 1♂, 18–31 December 1985 (S. & J. Peck) (AMNH). *Cape Province*: Table Mountain, Skeleton Gorge, 34°S, 18°30'E, 1♀, 13 February 1991 (V.D. & B. Roth) (CASC). **KENYA**: Rift Valley Province, Lake Naivasha, Fisherman's Camp, ca. 0°45'S, 36°20'E, 1♂, 19 October 1992 (V.D. & B. Roth) (CASC). **KENYA**: 49 mi NW of Mobasa, 450 m, 1♀, 4 November 1957 (E.S. Ross & R.E. Leech) (CASC). **TANZANIA**: NE side of Mt. Meru, 1500 m, 1♀, 28 October 1957 (E.S. Ross & R.E. Leech) (CASC). *Euprostenopsis armatus* (Strand 1913): **ZAIRE**: Garamba, 1♂ (AMNH). **ZIMBABWE**: Harare, 3♀, 14 August 1990 (V.D. & B. Roth) (CASC). *Eurychoera quadrimaculatus* Thorell 1897: **SINGAPORE**: MacRitchie Reservoir, 1♀ (Koh 77.01.01.01), 1♂ (Koh 88.020.06). *Paracladynis vis* Blandin 1979: **MADAGASCAR**: Antananarivo, 1♀, several juv., 13 February 1952 (V.J. Tipton) (AMNH); 2♀, 19 February 1992 (V. Roth) (CASC). *Mandraka*, 18°56'S, 47°56'E, 1♀, 10 March 1994 (W.J. Pulawski) (CASC). *Ranomafana*, I. Fanadiana town, 1♀, 16 May 1992 (Roth) (CASC). *Pisaura mirabilis* (Clerck 1757): **GERMANY**: Bayern, Spessart, Neuhütten, Zilch leg., 1♀, 19 June 1949 (AMNH ex SMFD). *Ransonia mahasoana* Blandin 1979: **MADAGASCAR**: Fianarantsoa Province, P.N. Ranomafana, Vohipara, 21°14'S, 47°24'E, 900 m, 2♀, 5–7 December 1993 (Scharff, Larcher, Griswold, Andriamasimanana) (currently CASC). *Antananarivo Province*, Amboh-

imanga, 18°44'S, 47°34'E, 1400 m, 2♂1♀, 1 November 1993 (Coddington, Larcher, Griswold, Andriamasimanana, Scharff) (currently CASC). *Antsiranana Province*, Marojeje Reserve, 8.4 km NNW Manantenina, 14°25'S, 49°45'E, 700 m, several ♂♀, 10–16 November 1993 (currently CASC). *Rothus purpurissatus* Simon 1898: **KENYA**: Lake Nakuru, N.P. campsite in Yellow Fever Forest, 1♀, 14 May 1975 (Penniman) (AMNH). **SOUTH AFRICA**: Natal, Lake Midmar, 1♂3♀, 6 January 1991 (V.D. & B. Roth) (CASC). *Tallonia picta* Simon 1889: **MADAGASCAR**: Province Antsiranana: Nosy Be, Lokobe Forest, 13°24'58.8"S, 48°18'26.5"E, 4♀, 11–14 August 1992 (V.D. & B. Roth) (CASC). Montagne d'Ambre, 12°30'57"S, 49°11'04"E, 2♀, 12 August 1992 (V.D. & B. Roth) (CASC). *Thalassiosops vachoni* Roewer 1955: **MADAGASCAR**: Maroantsetra, 1♂, SMFD RII/10552/102 (type-label carries an invalid manuscript name). *Vuattouxia* Blandin 1979 sp.: **MADAGASCAR**: Toamasina Province, P.N. Perinet, near Andasibe, 1000 m, 18°56'S, 48°24'E, 4♂5♀, 4–5 November 1993 (Coddington, Larcher, Griswold, Andriamasimanana, Scharff) (currently CASC); 18°55'S, 48°25'E, 1♂1♀, 1–3 August 1992 (V.D. & B. Roth) (CASC). *Chutes de la Mort*, 1♂, 10 November 1959 (E.S. Ross) (CASC). *Fianarantsoa Province*, P.N. Ranomafana, Talataky, 21°15'S, 47°25'E, 900 m, 5♀, 5–7 December 1993 (Scharff, Larcher, Griswold, Andriamasimanana) (currently CASC).

**Phylogenetics.**—The pisaurine genera *Charminus*, *Cispus*, *Tetragonophthalma*, *Afropisaura*, *Perenethis*, *Maypaci*, and *Polyboea* form the monophyletic *Perenethis* genus group, within the Pisaurinae as here defined. The synapomorphy for this genus group is the membranous saclike copulatory duct forming two large loops at least in some species of each of the seven genera except in *Cispus*. The genera *Charminus* and *Cispus*, themselves sister taxa, were designated as outgroup during the cladistic analysis (see above under METHODS). The sistergroup relationship between *Cispus* and *Charminus* is supported by the procurved carina, which is unique within the Pisaurinae. The outgroup genera were not newly revised for the present study and the character states of the type species of each genus were used in the cladistic analysis. However, most character states (Table 4) are identical in all known species of each genus as illustrated in Blandin's (1978a) revision of the genera. Characters of the internal female copulatory organ (*cha* 13–17) and a few character states in the male organs (*ch* 31, 33, 34),



not illustrated by Blandin, were assessed in two species in *Charminus* (*C. camerunensis* and *C. aethiopicus*). In *Cispis*, the male characters were assessed in three different species (*C. thorelli*, *C. problematicus* and *C. bidentatus*), the female characters are based on the type species alone (*C. variegatus*).

**Character description:** Somatic characters. Character 0: Number of cheliceral teeth; 0 = three teeth, 1 = four teeth (with occasional occurrence of three teeth at one of the chelicerae), 2 = two teeth. Three cheliceral teeth is the most common and widely distributed character state in the Pisaurinae and thus assumed to be the primitive condition (see Table 2). However, the character is somewhat homoplastic within the Pisaurinae, e.g., the state two teeth occurs in *Cispis bidentatus* (Lessert 1936), all other species of the genera *Charminus* and *Cispis* have three cheliceral teeth. Character 1: Size of cheliceral teeth; 0 = unequal, 1 = equal. The character displays homoplasy within this data set and outside (e.g., *Charminus ambiguus* (Lessert 1925) has three equally-sized teeth). Character 2: Shape of AER; 0 = recurved, 1 = straight, 2 = procurved, 3 = strongly procurved [= st proc I in Table 2], 4 = extremely procurved [= st proc II in Table 2]. The morphological difference in the AER in *Maypaci* and *Tetragonophthalma* justifies a separate coding (see Blandin's figures, 1974a, figs. 1, 4). Character 3: Size ratio of ALE to PME; 0 =  $ALE < PME$ , 1 =  $ALE = PME$ , 2 =  $ALE > PME$ . Character 4: Size ratio of ALE to AME; 0 =  $ALE < AME$ , 1 =  $ALE = AME$ , 2 =  $ALE > AME$ . Character 5: Patella spination; 0 = patella with one dorsal apical spine as in *Charminus* (Table 6), 1 = patella with two dorsal and two lateral spines as in *Afropisaura*, 2 = patella of legs I and II without spines, patella II and IV with a single dorsal apical spine, as in *Tetragonophthalma*. Character 6: Spine length, expressed as ratio of length of tibial spine of second ventral spine-pair to width of tibia; 0 = 3, 1 = 1–1.5, 2 = 6.5. Extremely long (state 2) or short spines (state 1) are not as common in Pisauridae as moderate spine length (state 0).

Female copulatory organ: Character 7: Trajectory of epigynal folds; 0 = anterior section of epigynal folds convergent and close together (Figs. 4, 6), 1 = anterior section of epigynal folds divergent and far apart (e.g., Figs. 17, 20). Character 8: Carina; 0 = continuous

(Figs. 4, 6, 17, 20, 23, 85, 88), 1 = separated into two distinct lateral, nearly straight branches (e.g., Fig. 31). Character 9: Carina form; 0 = recurved (Figs. 17, 20, 23, 82), 1 = straight (e.g., Figs. 31, 88), 2 = procurved as in the outgroup (Figs. 4, 6), 3 = undulated as in *Tetragonophthalma* (Fig. 23), 4 = undulated as in *Perenethis symmetrica* (Fig. 34). A recurved carina (state 0) occurs in many pisaurine spiders. Character 10: Posterior edge of carina; 0 = ridgelike (e.g., Fig. 31), 1 = liplike, overhanging anterior section of epigynal folds (e.g., Figs. 17, 23, 88). Character 11: Anterior edge of carina; 0 = weakly developed (Figs. 4, 6), 1 = distinctly developed, ridgelike (e.g., Figs. 17, 20, 31, 82, 85, 88). Character 12: Position of fossae in relation to copulatory opening; 0 = directly above copulatory openings (Figs. 17, 20, 23), 1 = above and lateral to copulatory opening (e.g., Figs. 4, 6, 42, 45), 2 = above and between copulatory openings (Figs. 82, 85, 88). Fossae directly above the copulatory openings appear to prevail in the Pisaurinae, thus this state is coded as 0. Character 13: Copulatory duct; 0 = membranous (e.g., Figs. 532, 35, 89), 1 = posterior section sclerotized (Figs. 83, 84), 2 = anterior and posterior sections sclerotized with membranous middle section (Figs. 18, 21), 3 = fully sclerotized over its entire length (*Tetragonophthalma*, Fig. 23). Character 14: Number of loops of copulatory duct; 0 = single loop (Figs. 7, 83, 86), 1 = two loops (e.g., Figs. 5, 32, 35, 89), 2 = two and one half loops (Figs. 18, 21, 24). Character 15: Copulatory duct loop sizes; 0 = first loop larger than second loop (e.g., Figs. 5, 49, 89), 1 = first loop equal to second loop (Figs. 24, 35). Character 16: Position of head of spermatheca; 0 = pointing laterally (e.g., Figs. 5, 19), 1 = pointing anteriorly (e.g., Figs. 7, 22), 2 = bent (Fig. 33). In the bent position, the *hs* points anteriorly, but the stalk immediately behind it is bent, thus the spermathecal duct does not run straight in that section. Character 17: Spermathecal base; 0 = with large lumen (Figs. 7, 22, 38, 41, 44, 47, 50), 1 = with small lumen, does not fill base of spermatheca (Figs. 5, 33, 35, 90), 2 = base filled with loops of spermathecal duct (Figs. 19, 24). Displays homoplasy within the genera *Afropisaura*, *Perenethis*, and *Maypaci*.

Male copulatory organ: Characters for the male of *Maypaci kaestneri* were taken from



Table 4.—Character scoring. The character matrix does not contain autapomorphies of terminal taxa (e.g., flap at the conductor in *Charminus*), unless they are part of a multistate series. Non-applicable character states indicated by “—”. Unknown character states indicated by “?”.

	<i>Ch. camerunensis</i>	<i>Ci. variegatus</i>	<i>A. valida</i>	<i>A. ducis</i>	<i>T. vulpina</i>	<i>Pe. simoni</i>	<i>Pe. symmetrica</i>	<i>Pe. dentifasciata</i>	<i>Pe. sindica</i>	<i>Pe. venusta</i>	<i>Po. vulpina</i>	<i>M. roeweri</i>	<i>M. kaestneri</i>	<i>M. petrunkovitchi</i>
Somatic characters														
0) Cheliceral teeth #: 3; 4(3); 2	0	0	0	0	1	2	2	2	2	2	2	2	2	2
1) Chel. teeth size: unequal; equal	0	0	1	1	1	0	0	0	0	0	1	1	1	1
2) AER rec; str; proc; strongly proc; extremely proc	0	0	1	2	3	2	2	2	2	2	2	4	4	4
3) ALE<PME; ALE=PME; ALE>PME	0	0	0	0	1	0	0	0	0	0	2	1	1	1
4) ALE<AME; ALE=AME; ALE>AME	1	0	1	2	2	0	0	0	0	0	2	0	0	0
5) Patellar spines: 1; 4; 0 and 1	0	0	1	1	2	0	0	0	0	0	0	0	0	0
6) Spine length to tibia width: 3;1–1.5; 6.5	0	0	0	0	1	0	0	0	0	0	2	1	1	1
Female characters														
7) anterior <i>epf</i> : convergent; divergent	0	0	1	1	1	1	1	1	1	1	1	?	1	1
8) carina: continuous; two branches	0	0	0	0	0	1	1	1	1	1	0	?	0	0
9) carina: rec; str; proc; <i>Tetragonophthalma</i> ; <i>P. symmetrica</i>	2	2	0	0	3	1	4	1	1	1	1	?	1	0
10) Posterior edge of <i>ca</i> : ridge; lip	0	1	1	1	0	0	0	0	0	1	?	0	0	0
11) anterior edge of <i>ca</i> : weak; strong	0	0	1	1	1	1	1	1	1	1	1	?	1	1
12) position of fossae: directly above copulatory openings; lateral; between	1	1	0	0	0	1	1	1	1	1	2	?	2	2
13) copulatory duct: membranous; posterior section sclerotized; posterior and anterior section sclerotized; fully sclerotized	0	3	2	2	3	0	0	0	0	0	0	?	0	1
14) <i>cd</i> loops: 1; 2; 2½	1	0	2	2	2	1	1	1	1	1	1	?	0	0
15) <i>cd</i> loop sizes: 1 > 2; 1 = 2;	0	—	0	0	1	0	1	0	0	0	0	?	—	—
16) <i>hs</i> position: lateral; anterior; bent	0	1	0	1	1	2	2	0	2	2	2	?	2	1
17) <i>bs</i> : large lumen; small lumen; lumen filled with duct loops	1	0	2	0	2	1	1	0	0	0	1	?	0	1
Male characters														
18) <i>rta</i> shape: round-perpendicular; flat-forward	0	0	0	0	0	1	1	?	1	1	0	1	0	?
19) <i>rta</i> tip: pointed; rounded	0	0	0	0	1	1	1	?	0	0	0	0	?	?
20) tibial venter: smooth; with hump	0	0	0	0	0	1	1	?	1	1	0	0	0	?
21) tegulum base: smooth; with peak	0	0	0	0	0	1	1	?	1	1	1	1	1	?
22) <i>c</i> tip: long; short	0	0	1	1	0	0	0	?	0	0	0	0	0	?
23) <i>c</i> midpiece: long; short	0	0	0	0	0	0	0	?	0	0	0	1	1	?
24) <i>c</i> tip: broad round; slender round; spiral; modified spiral	0	0	—	—	0	1	1	?	1	1	2	3	3	?
25) <i>c</i> base: narrow; broad	0	0	1	1	1	0	0	?	0	0	0	0	0	?
26) <i>c</i> mesally: smooth; with hump	0	0	0	0	0	1	1	?	1	1	0	0	0	?
27) <i>c</i> tip: with ridge-like fold; smooth	0	0	1	1	0	1	1	?	1	1	0	0	0	?
28) <i>c</i> tip: additional guiding lamella absent/present	0	0	0	0	0	0	0	?	0	0	1	1	1	?
29) <i>db</i> of <i>da</i> smooth; with pit	0	0	0	0	0	0	0	?	0	0	1	1	?	?
30) scl A size: small; median; large	1	1	1	1	0	0	0	?	0	0	2	2	?	?
31) scl A shape: triangular; rod; small, oval; forked	0	0	3	1	1	2	2	?	2	2	3	3	?	?
32) <i>dst</i> shape: <i>Ch</i> ; <i>Ci</i> ; <i>Afro</i> ; <i>Tetra</i> ; <i>Pe</i> ; <i>PoMay</i>	0	1	2	2	3	4	4	?	4	4	5	5	?	?
33) <i>e</i> length: long; moderate; short	0	1	0	0	0	0	0	?	0	0	1	2	2	?
34) <i>pp</i> length: short; ½ to ¾; total <i>e</i> length	0	2	1	1	1	1	2	?	1	1	0	1	?	?

Blandin's figure (1975a: 389, figs. 21, 22). Character 18: Retrolateral tibial apophysis (RTA); 0 = round and perpendicular to palpal tibial (e.g., Figs. 9, 12–15, 25, 27, 97), 1 = flat and parallel to cymbium (e.g., Figs. 54–59, 91). Character 19: Tip of RTA; 0 = pointed (e.g., Figs. 14, 59), 1 = rounded (Figs. 28, 56, 58). Character 20: Tibial venter; 0 = smooth (e.g., Figs. 11, 15, 92, 97), 1 = with hump-shaped apophysis (Figs. 54, 55, 58, 79). Character 21: Tegulum base; 0 = smoothly rounded (e.g., Figs. 8, 10, 25, 29), 1 = with basal protuberance at retrolateral side of unexpanded bulb (unique within the Pisaurinae, Figs. 54, 92, 97). Character 22: Conductor tip length; 0 = long (e.g., Figs. 10, 58), 1 = short (Fig. 25). Character 23: Conductor midpiece between tip and base; 0 = long (e.g., Figs. 13, 55, 57), 1 = short (Figs. 91, 95). Character 24: Conductor tip shape; 0 = broad and well rounded (Figs. 10, 12, 27) as in the outgroup, 1 = slender and rounded as in *Perenethis* (Figs. 54–58), 2 = modified, with a spiral tip as in *Polyboea* (Figs. 97, 98), 3 = modified as in *Maypaci* (Fig. 93). Character 25: Base of conductor; 0 = narrow (Figs. 55, 95, 98), 1 = broad (Figs. 26, 28). Character 26: Conductor mesal margin; 0 = smooth, 1 = with mesal inflatable hump as it occurs in *Perenethis* (Fig. 55). Character 27: Conductor tip folds; 0 = conductor tip with a ridgelike fold formed by the membranous inner conductor wall as in *Charminus* and *Tetragonophthalma* (Fig. 10, 12, 27), 1 = inside of tip smooth (Fig. 56). Character 28: Posterior guiding lamella at tip of conductor; 0 = absent (Fig. 10), 1 = present (Figs. 95, 98). Character 29: Dorsal branch of distal tegular apophysis; 0 = smooth, 1 = with pit (Figs. 95, 98). The morphological similarity in the distal tegular apophysis between *Polyboea* and *Maypaci* is striking and links both genera. Character 30: Size of sclerite A; 0 = small (Fig. 29), 1 = medium (Figs. 11, 14, 15), 2 = large (Figs. 94, 99). This sclerite can only be seen in the expanded bulb. As far as known, a small sclerite A is widely distributed within the Pisaurinae. Character 31: Sclerite A shape; 0 = triangular, as in *Charminus* and *Cispius* (Figs. 11, 14), 1 = rod-shaped, as in *Tetragonophthalma* (Fig. 29), 2 = small, elongated oval, as in *Perenethis*, 3 = large, one end forked as in *Afropisaura valida*, *Polyboea* and *Maypaci* (Figs. 91, 93, 99). Character 32: Shape of

sclerotized tube of embolic division; 0 = as in *Charminus*, 1 = as in *Cispius*, 2 = as in *Afropisaura*, 3 = as in *Tetragonophthalma*, 4 = as in *Perenethis*, 5 = as in *Polyboea* and *Maypaci*. Character 33: Embolus length; 0 = long (Figs. 11, 25, 26, 28, 54, 57), 1 = moderate (Fig. 14, 99), 2 = short (Fig. 95). Character 34: Length of pars pendula alongside the embolus; 0 = short (Figs. 11, 99), 1 =  $\frac{1}{2}$ – $\frac{3}{4}$  along the embolus (Figs. 26, 28, 56), 2 = total embolus length to its tip (Figs. 14, 15, 58).

*Analysis.* Hennig86 runs containing all characters (multistate characters unordered) resulted in three equally parsimonious, highly resolved trees of 87 steps, with a consistency index (*ci*) of 0.72 and a retention index (*ri*) of 0.76, differing only in the resolution of the three species of the genus *Maypaci*. The equally long Nelson Consensus Tree (Fig. 2), is part of the original series of three trees, and places these three species in an unresolved trichotomy. An inspection of the other two, mutually exclusive trees presenting the three species fully resolved, showed that the resolution is based on presumed character states of missing characters. Only in two of the nine species of the genus *Maypaci* are the males and females known, and few specimens are available for study (see below under *Maypaci*), causing this lack of data. Optimization of character-state changes may differ with the choice of optimization schemes, ACCTRAN (depicted here in Fig. 2) or DELTRAN. In the following description, only non-homoplastic character-state changes supporting a clade under both optimization schemes are discussed, unless noted otherwise.

The Ingroup (clade A), containing the genera *Tetragonophthalma*, *Afropisaura*, *Perenethis*, *Maypaci*, and *Polyboea* is defined by the following synapomorphies of non-homoplastic character-state changes: Procurved anterior eye row (*ch* 2), the shape of epigynal folds (*ch* 7), the strongly developed anterior edge of the carina (*ch* 11), and a pars pendula  $\frac{1}{2}$ – $\frac{3}{4}$  along the embolus (*ch* 34). The genera *Afropisaura* and *Tetragonophthalma* (clade B) form the sister-group to clade C. The sister-group relationship between *Afropisaura* and *Tetragonophthalma* is supported by five non-homoplastic character-state changes: The position of the fossae above the copulatory openings (*ch* 12), the undulated posterior sec-



Table 5.—Character performance. \*Different optimizations ACCTRAN/DELTRAN.

Character number	Character states	Steps	ci	ri
0)	m (3)	2	100	100
1)	b	2	50	83*
2)	m (5)	4	100	100
3)	m (3)	3	66	66*
4)	m (3)	4	50	33
5)	m (3)	2	100	100*
6)	m (3)	3	66	66*
7)	b	1	100	100
8)	b	1	100	100
9)	m (5)	5	80	66*
10)	b	2	50	66
11)	b	1	100	100
12)	m (3)	2	100	100
13)	m (4)	4	75	50*
14)	m (3)	3	66	75
15)	b	2	50	0
16)	m (3)	5	40	40
17)	m (3)	5	40	40
18)	b	2	50	75
19)	b	2	50	50
20)	b	1	100	100
21)	b	1	100	100
22)	b	1	100	100
23)	b	1	100	100
24)	m (4)	3	100	100*
25)	b	1	100	100
26)	b	1	100	100
27)	b	2	50	80
28)	b	1	100	100
29)	b	1	100	100
30)	m (3)	3	66	75*
31)	m (4)	4	75	75*
32)	m (6)	5	100	100*
33)	m (3)	3	66	50*
34)	m (3)	4	50	0*

tion of the copulatory duct (*ch* 14), copulatory duct with 2½ loops), spermathecal base filled with loops of spermathecal duct (*ch* 17, reversal in *Afropisaura* ducts), the broad base of the conductor (*ch* 25), and the rod-shaped sclerite A (*ch* 31). Non-homoplastic apomorphies for the genus *Afropisaura* are the spination of the patella (*ch* 5), the partly sclerotized copulatory duct (*ch* 13), the short pointed conductor (*ch* 22), and—under DELTRAN optimization—the peculiar shape of the distal sclerotized tube of the embolic division (*ch* 32). Clade C (sister taxon to clade B), containing the genera *Perenethis*, *Polyboea* and *Maypaci* is supported by the loss

of one cheliceral tooth (*ch* 0), the straight carina (*ch* 9, with special form in *P. symmetrica* and recurved carina in *M. petrunkevitchi* Lessert 1933), the bent spermathecal head (*ch* 16, with reversals in *P. symmetrica* and *M. petrunkevitchi*), and the basal protuberance at the tegulum (*ch* 21). The sister-group relationship of *Polyboea* and *Maypaci* (clade D) is corroborated by mesal position of the fossae (*ch* 12), the additional guiding lamella in the conductor (*ch* 28), the pit in the dorsal branch of the distal tegular apophysis (*ch* 29), the large, forked sclerite A (*ch* 30), and—under ACCTRAN optimization—the shape of the distal sclerotized tube of the embolic division (*ch* 32). The species of *Maypaci* included in this study are defined by the strongly procurved anterior eye row (*ch* 2), the short conductor midpiece (*ch* 23), and—under ACCTRAN—the short embolus (*ch* 34).

The genus *Perenethis*, the sister taxon of clade D, is defined by four apomorphies of non-homoplastic character-state changes: Carina with two branches (*ch* 8), the ventral tibial apophysis (*ch* 20), the slender, rounded tip of the conductor (*ch* 24), the mesal hump at the conductor (*ch* 26), and—under DELTRAN—the shape of the distal sclerotized tube of the embolic division (*ch* 32). The sister-group relationship of the African species, *Perenethis simoni* and *Perenethis symmetrica*, is weakly supported by a homoplastic character-state change, the rounded tip of the retrolateral tibial apophysis (*ch* 19). The Asian-Australian species of the genus are weakly supported by the large lumen in the spermathecal base (*ch* 17), a very homoplastic character throughout the Pisaurinae. The cladogram clearly demonstrates that the astounding phenetic similarity between *P. simoni* (Lessert 1916), *P. sindica* (Simon 1897) and *P. venusta* L. Koch 1878 is based on symplesiomorphies alone and suggests, however weakly, that the African species and the Asian species of *Perenethis* form separate clades.

**Zoogeography.**—Pisaurine genera are predominantly African (south of the Sahara), but one genus, *Polyboea*, is restricted to south-east Asia. *Pisaura* itself occurs in Europe and Asia. The distribution patterns within the Pisaurinae display an interesting peculiarity: Three genera, *Perenethis*, *Dendrolycosa* (genus unrevised, Blandin 1979a, figs. 30, 34, 36)

Table 6.—Leg spination patterns of *Charminus*, typical for the Pisaurinae. Genus specific variations shown below. Abbreviations: 1 = average size spine; i = short spine; I = long spine; \* = spine dislocated to retrolateral; v = spine dislocated to ventral; 2 = spine pair, average length; ii = spine pair, spines short. Notation indicates location of spine on leg segment, e.g., proximal, apical, and to other spines of segment. Spine length [ventral tibial spine, second pair, first leg]: spine length : tibia width = 3 set as normal length.

*Charminus*

leg	do	Fe	1	1	1	Pa	1	Ti	1 <sup>*</sup>	1	Me	ii				
I	pl	i	0	0	I	1				1	1 <sup>v</sup>	1	1	1		
	rl	1	1	1	1	1				1	1	1	1	1		
	v									2	2	2	ii	2	2	i
leg	d	Fe	1	1	1	Pa	1	Ti	1 <sup>*</sup>	1	Me	ii				
II	pl	1	1	1	1	1				1	1 <sup>v</sup>	1	1	1		
	rl	1	1	1	1	1				1	1	1	1	1		
	v									2	2	2	ii	2	2	i
leg	do	Fe	1	1	1	Pa	I	Ti	1 <sup>*</sup>	1	Me	ii				
III	pl	1	1	1	1	1				1	1 <sup>v</sup>	1	1	1		
	rl	1	1	1	1	1				1	1	1	1	1		
	v									2	2	ii	2	2	i	
leg	do	Fe	1	1	1	Pa	1	Ti	1 <sup>*</sup>	1	Me	ii				
IV	pl	i	i	1	1	1				1	1 <sup>v</sup>	1	1	1		
	rl	0	0	0	1	1				1	1	1	1	1		
	v									2	2	ii	2	2	i	

*Afropisaura*

leg	do	Fe	1	1	1	I-IV	Pa	i	1
I	pl	0	1	1	I	1		i	
	rl	1	1	1	1	1		i	

*Tetragonophthalma*

leg	do	Fe	1	1	i	I, II	Pa	0	III, IV	Pa	1.
I	pl	i	1	1	I	1					
	rl	1	1	1	1	1					
♀	leg	do	Ti	0	III, IV	Ti	1*	1			
I, II	pl	1	1 <sup>v</sup>	1	1			1	1		
	rl	1	1	1	1			1	1		
	v	2	2	2	ii	2	2	ii	2	2	ii
♂	leg	do	Ti	(1*)	1	III, IV	Ti	1*	1		
	pl	1	1 <sup>v</sup>	1	1 <sup>v</sup>	1	1	1	1 <sup>v</sup>		
	rl	1	1	1	1	1	1	1	1		
	v	2	2	2	ii	2	2	ii	2	2	ii

*Polyboea*

leg	do	Fe	1	I	i	I-IV	Ti	1*	1
I	pl	0	I <sup>v</sup>	I <sup>v</sup>	I <sup>v</sup>	1	1	1 <sup>v</sup>	1
	rl	1	1	1	1	1	1	1	1
	v					2	2	2	0



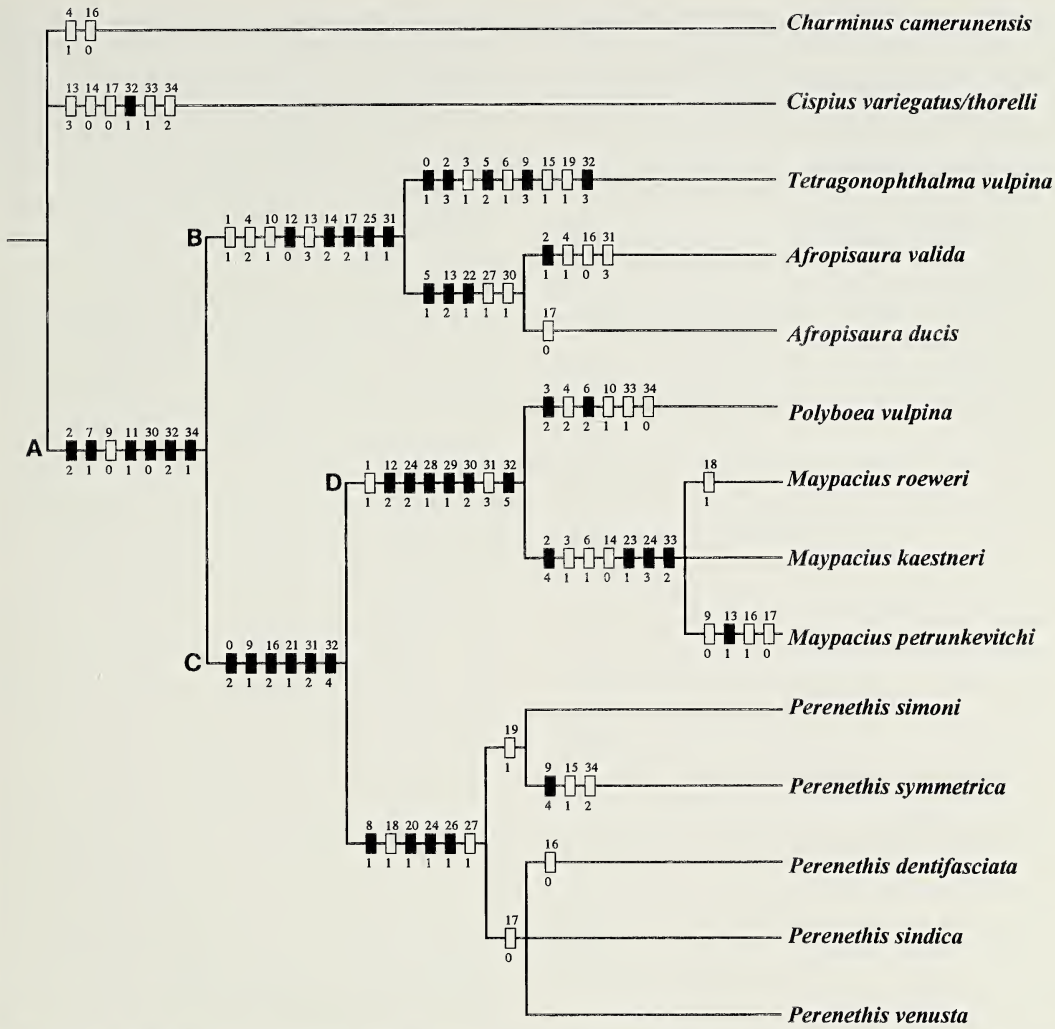


Figure 2.—Preferred Cladogram (identical to Nelson Consensus Tree). ACCTRAN character optimization; character mapping: black rectangles = non-homoplastic character state origination, white rectangles = homoplastic character state origination [implemented in CLADOS by setting homoplasy indicator, HOM=0].

and *Euprosthénops* (Blandin 1975b), contain both African and Asian species.

In the genus *Perenethis*, two species, *P. simoni* and *P. symmetrica*, occur in Africa (Fig. 3); three species, *P. sindica*, *P. dentifasciata* and *P. fascigera* are distributed in Asia (including India and Sri Lanka); and one species, *P. venusta* occurs in Australia and the Bismarck-Archipelago. *Maypacius*, the sister taxon of the Asian genus *Polyboea*, is restricted to Africa. This specific pattern, the distribution of closely related species in Africa south of the Sahara and Asia/Australia, can be found in other Pisauridae *sensu*

*lato* as well. The pisaurid genus *Thalassius*, presumably a relative of the worldwide genus *Dolomedes*, shows a similar pattern. Eight species of the genus *Thalassius* occur in Africa, and four species in Madagascar. A single species, *T. jayacari* F.O. Pickard-Cambridge 1898, is found in the Middle East; and two species, *T. albocinctus* (Dolescall 1859) and *T. phipsoni* F.O. Pickard-Cambridge 1898, are distributed in south-east Asia, including China, the Philippines and Singapore (Sierwald 1987). There are other groups displaying an African-Southeast Asian distribution of close relatives, e.g., the tropical

tree-frog subfamily Rhacophorinae (family Ranidae) (Savage 1973), the genus *Francolinus* among the galliform birds (Dinesen et al. 1994), several members of the bird family Rallidae (Olson 1973), and members of the plant family Sapotaceae (Pennington 1991).

Africa, South America and India (together with Madagascar) formed a contiguous land mass about 155 million years before present. Madagascar separated from Africa over 120 m.y.b.p. and South America separated from Africa about 95 m.y.b.p. (Smith et al. 1994). Since no member of the *Perenethis* genus group has been recorded from Madagascar or the Americas so far, it is unlikely that the origin of the terminal taxa studied here dates back more than 100 million years. When optimizing the current distribution of the terminal taxa like a character on the proposed cladogram (Fig. 3) it is most parsimonious to assume an African origin for the group. Using Bremer's (1992) method to reconstruct the ancestral area of the group under study here, yields the same result. Assuming an African distribution of early pisaurine taxa requires a hypothesis regarding the presence of *Polyboea* and *Perenethis* in Asia and Australia. Two independent events, one in clade D and another within *Perenethis*, have to be proposed to account for the current distribution pattern. According to Axelrod & Raven (1978), lowland rain forest and subtropic rain forest covered most of Africa during the Paleocene (60 m.y.b.p.), thus ancestors of the group under study were likely to be more widely distributed in Africa than today, where they are mostly restricted to Africa south of the Sahara. At that time, the Tethys Sea was an effective barrier between Africa and Asia. In the mid-Miocene (15 m.y.b.p.) a land bridge formed between Africa and Arabia, connecting the African land mass with Asia. During the Miocene, the exchange of mammalian taxa between Africa and Asia increased dramatically presumably via this land bridge, resulting in a significant decrease of mammalian taxa endemic to Africa in the Pliocene. A two-way traffic via the Arabian Peninsula affected the composition of both faunas in Asia and Africa (Maglio 1978). The habitat conditions along that passage-way were suitable at various times during the Cenozoic for many large mammals, indicating the existence of vegetation cover. Savage (1973) explains the Afri-

can-Asian distribution of the tropical tree-frog subfamily Rhacophorinae (Family Ranidae) as an immigration from Africa to Asia during the early Cenozoic. Dinesen et al. (1994) also assume that the African-Asian distribution of several related forest birds can be explained by alternations of isolation and range expansion opportunities via an African-Arabian land bridge to Asia.

The blockage of the Tethys Sea by a land bridge between Africa (including Arabia) and Asia in the mid-Miocene (15 m.y.b.p.) with subsequent alteration of the latitudinal air-ocean circulation produced a drier climate in northern Africa (Crowell & Frakes 1970) and caused the expansion of savanna and sclerophyll vegetation over northern Africa and the Sahara region (Axelrod & Raven 1978). The hot, dry Saharan-Libyan desert did not develop before the Pleistocene. To my knowledge, no Pisauridae *sensu lato* have been reported from very arid habitats. Judging from their current habitat preferences, deserts and high mountainous areas may be the most difficult areas to cross, thus presenting effective barriers. The restriction of most pisaurine taxa to the south of the Sahara supports this notion. At least two independent events have to be assumed for the *Perenethis* genus group to account for the occurrence of species of this group in Asia. Instead of invoking hypotheses of chance dispersal (e.g., ballooning) over pre-existing barriers like the Sahara, range expansions of the respective ancestral species by tracking the expansion of suitable habitats across the mid-Miocene (15 m.y.b.p.) land bridge between Africa (including Arabia) and Asia via Iran before the development of the Sahara may be more plausible. From the end of the Pliocene until today, the expansion of the Sahara formed an increasingly effective barrier to animal migration (Coryndon & Savage 1973). Thus, two independent range extension events are proposed, most likely between the mid Miocene and beginning of the Pleistocene, during the emergence of clade D and the emergence of the genus *Perenethis* which caused the African-Asian distribution of these clades.

## TAXONOMY

### Discrimination of morpho-species.—

When working on the alpha-taxonomic level of poorly known groups for which only pre-



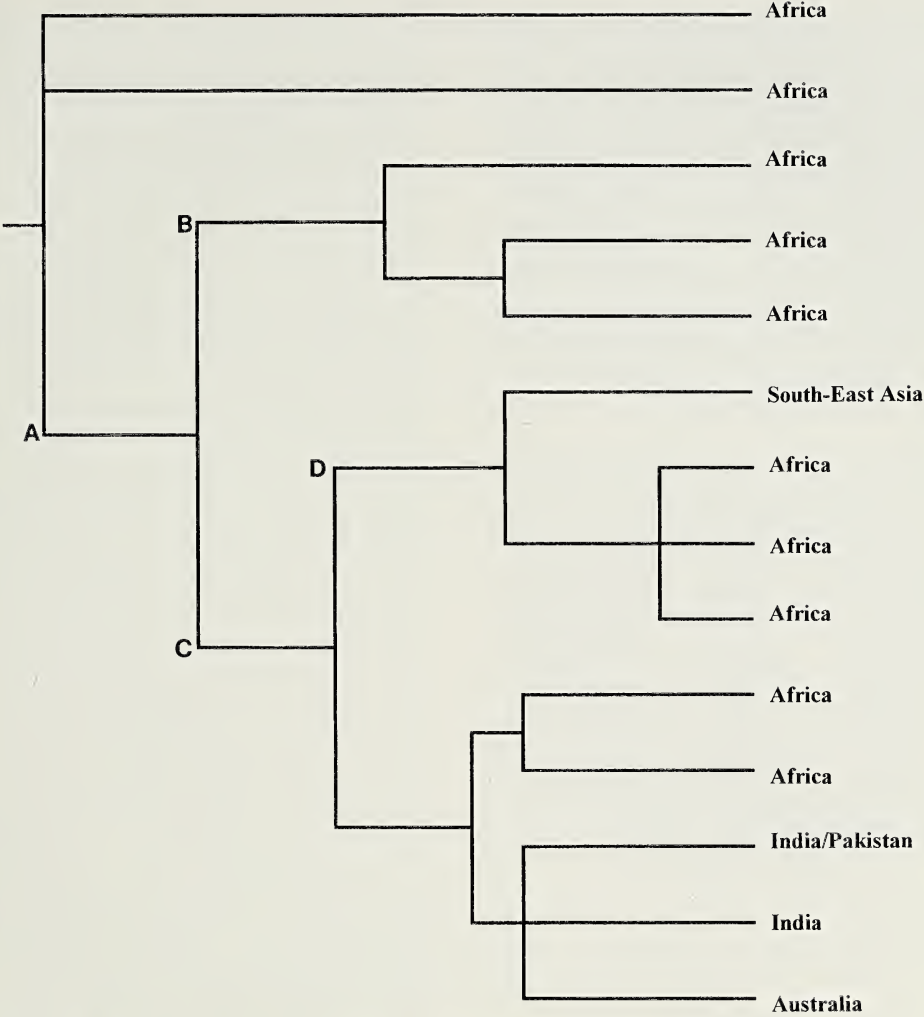


Figure 3.—Area cladogram, taxon names replaced by their distribution.

served material is available, the discrimination of “morpho-species” as a reasonable assessment of biological species becomes the practical solution. In the species revisions of the genera *Perenethis* and *Tetragonophthalma* below, I diverge in some cases quite remarkably from species delimitations drawn by previous authors, mainly Roewer (1955), but also Blandin (1974a—1979b). For this reason it appears to be appropriate to present the rationale for morpho-species delimitations employed in this study. A species-typical trait (= character or character state) should: a) occur consistently in all members of the species, b) be qualitatively discrete (= variation should not show continuous overlap among organisms assigned to different species), and c) prefera-

bly show congruence with at least one other such trait. Studies on individual variability within samples and/or populations, whenever feasible, should be considered. In most spider groups, discrete traits in the male palpal organ, e.g., shape of median apophysis or tibial apophysis, are good indicators for the recognition of distinct species. Which structural part of the male palpal organ reveals species-typical attributes varies among closely related spider groups, e.g., at the generic level. The retrolateral tibial apophysis, the median apophysis, the conductor and, within the Pisaurinae, the distal tegular apophysis, are often species-typical.

The female epigynum can show quite a range of variation within a species, which led

to numerous redundant species descriptions, e.g., *Thalassius spinosissimus* (Karsch 1878) with its 40 junior synonyms (Sierwald 1987). The ducts and spermathecae of the vulva show less individual variability and are therefore more reliable features for the discrimination of species, at least in all Pisauridae I have examined so far, e.g., the shape of the head of spermathecae in *Thalassius* (see Sierwald 1987). For alpha-taxonomic studies of spiders, the structure of the vulva should always be included if females are available. Within the species studied for the present paper, the duct leading from the head to the base of the spermathecae may show variations in its loops, even differing between the left and right sides of a single individual. Subadult females with heavily sclerotized pre-epigyna (primordia of the developing copulatory organs, Sierwald 1989b) have been mistaken for adults and consequently caused the description of synonymous taxa or *nomina dubia* as in *Maypaci- us bilineatus* (Pavesi 1895), see Blandin 1975a. Congruence of discrete traits in both male and female copulatory organs permit reliable species-discrimination. Somatic features, such as color-pattern, eye-pattern, spination and leg formula that occur consistently in concordance with discrete traits of copulatory organs of one of both sexes furnish additional species-typical attributes. Somatic features often facilitate recognition of conspecific sexes, but may display sexual dimorphism (see *Tetragonophthalma* below). From my experience with Pisauridae, coloration and color-pattern are prime candidates for sexual dimorphism and polymorphism within species. However, there are noteworthy exceptions such as the color pattern in both sexes of *Perenethis symmetrica* which is consistently different from all other species of the genus.

**Taxonomic history of the *Perenethis* genus group.**— The *Perenethis* genus group comprises the pisaurine genera *Charminus*, *Cispis*, *Tetragonophthalma*, *Afropisaura*, *Perenethis*, *Maypaci- us*, and *Polyboea*. The African genera *Charminus* and *Cispis* are morphologically similar and have been confused in the past. Blandin (1978a) separated both genera conclusively by features of the eye pattern, the tibial apophysis and the embolus, and moved several species originally described in *Cispis* to *Charminus*. The gen-

era *Tetragonophthalma*, *Perenethis* and *Maypaci- us* each have caused taxonomic problems and misinterpretations since their introduction to arachnology (comprehensive review by Blandin 1974a). Several species were shifted mainly among the three genera [e.g., *Maypaci- us bilineatus*, described *sub Tetragonophthalma*], probably due in part to the homogeneity of certain morphological features (especially the structure of the epigynum) and in part due to misidentification of genus-typical characters (e.g., retromarginal cheliceral teeth). The major event causing confusion was an incorrect re-description of the genus *Tetragonophthalma* by Simon (1898a), in which he cited two retromarginal cheliceral teeth. Karsch (1878), in the original description of *Tetragonophthalma*, did not give the number of teeth at the posterior margin of the chelicerae. Dahl (1908) examined the holotype of *Tetragonophthalma phylla* Karsch 1878 (type species of the genus), noted four cheliceral teeth, and rejected Simon's synonymy of *Perenethis* with *Tetragonophthalma*. Meanwhile, Simon (1898) had introduced the genus *Phalaea* to accommodate species with four teeth at the posterior margin of the chelicerae, thus creating a junior synonym for *Tetragonophthalma*. Subsequent authors either followed Simon's interpretation of the genus *Tetragonophthalma* [e.g., Bösenberg & Strand 1906 in the description of *Perenethis fascigera* under *Tetragonophthalma*] or rejected it (Pocock 1900). Roewer (1955) reviewed the issue and re-examined the immature type of *T. phylla* (which apparently has been lost since; *vide* Blandin 1976a). The genus *Afropisaura* was recently described by Blandin (1976b) for three African species formerly placed in the genus *Pisaura*. The monotypic genus *Polyboea* was introduced by Thorell (1895) for a juvenile male from Burma. Male and female of the type species are figured here for the first time.

#### *Charminus* Thorell 1899

Figs. 4, 5, 8–11

*Charminus* Thorell 1899: 83. Type species, by original designation, *Charminus camerunensis* Thorell 1899: 83; ♂ ♀, Cameroon.

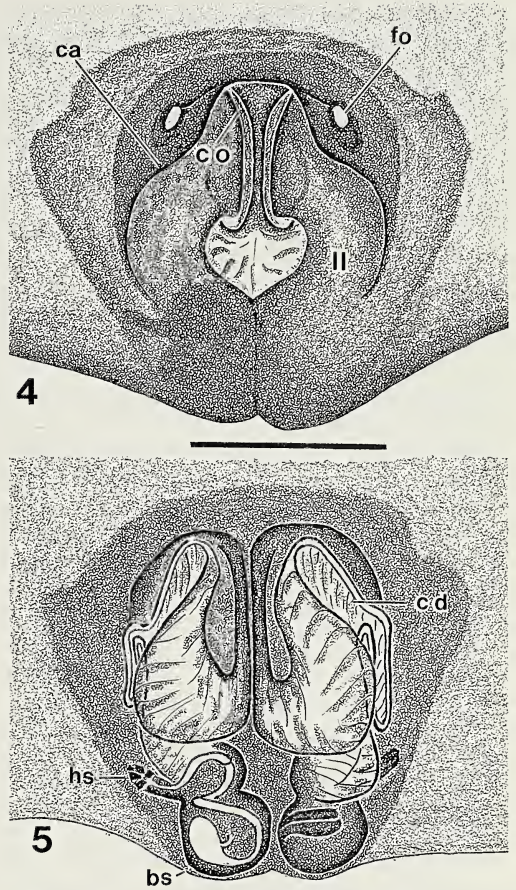
Nine species are currently recognized in the genus; two species are known from females only, one is known from a single male. Valid species of the genus: *Charminus aethiopicus*



Caporiacco 1939, ♂ ♀ known; *Cispius ambiguus* Lessert 1925, ♂ ♀ known; *Cispius atomarius* Lawrence 1942, ♂ ♀ known; *Charminus bifidus* Blandin 1978 (1978a), ♂ known; *Charminus camerunensis* Thorell 1899, ♂ ♀ known; *Cispiolus marfieldi* Roewer 1955, ♂ ♀ known; *Cispius minor* Lessert 1928, ♂ ♀ known; *Cispius natalensis* Lawrence 1947, ♀ known; *Charminus rotundus* Blandin 1978 (1978a), ♀ known.

**Diagnosis.**—AER recurved (*ch* 2), three cheliceral teeth (*ch* 0); epigynal folds anteriorly parallel and close to each other (*ch* 7), carina procurved (*ch* 9); conductor with narrow basal stalk (*ch* 25) and broad, rounded, flaplike apical section (*ch* 24); single guiding fold for embolus (*ch* 27); embolus long and whip like (*ch* 33). Autapomorphic characters: AE nearly same size as PE (*ch* 3), lateral flap at conductor, carina with lateral lobes. Synapomorphic characters: Procurved carina as in *Cispius* (*ch* 9). The membranous saclike copulatory duct forming two loops (*ch* 14) occurs at least in some species of the following pisaurine genera: *Afropisaura*, *Perenethis*, and *Polyboea*; in *Tetragonophthalma*, the two loops are sclerotized (*ch* 13) but their shape and trajectory are identical to *Afropisaura*. The copulatory ducts in other pisaurine genera are different, as far as currently known.

**Description of *Charminus camerunensis* Thorell 1899.**—(2♂1♀). *Measurements*: ♀ slightly larger than ♂, ♂ with longer legs than ♀. ♀ body 7.8–9.7 long, prosoma 2.8–3.5 long, 2.5–2.9 wide. Leg length: (prosoma 3.5 long) Fe 5.2, PaTi 6.5, MeTa 7.5, total length 19.5. ♂ body 8.7 long, prosoma 3.5 long, 2.7 wide. Leg length: Fe 6.3, PaTi 8, MeTa 9.8; total length 24.1. Eye pattern: AER recurved and only slightly shorter than PER, AE slightly smaller than PE, PME:AME = 1.2; ALE slightly smaller than AME or AME=ALE. Chelicerae: Posterior margin dentition somewhat variable even within individuals, mostly with three, some individuals with four teeth; teeth unequal in size, equally-sized in *Charminus ambiguus*. Spine pattern: See Table 6. Epigynum (Fig. 4): Epigynal folds parallel and close together anteriorly, curved in the middle section, adjoining in the posterior section; entire carina procurved; posterior edge ridgelike, anterior edge indistinct; fossae lateral to copulatory openings. Vulva (Fig. 5): Copulatory duct membranous, two loops, first



Figures 4, 5.—*Charminus camerunensis* from Gabon. 4, Epigynum; 5, Vulva. Scale line = 0.5 mm.

loop larger than second, head of spermatheca pointing laterally, spermathecal duct with one loop, base of spermatheca bulbous, with small lumen. Male palp (Figs. 8–11; Sierwald 1990, figs. 49–50): Retrolateral tibial apophysis simple, perpendicular, tip pointed; conductor base narrow, apical section broad with genus-typical flap (Blandin 1978a: figs. 22–27) and single low guiding fold; median apophysis with S-shaped hook; distal tegular apophysis with wing and hook; base of dst with two ridges, embolus long, pars pendula  $\frac{1}{3}$  of embolus length.

**Taxonomic note.**—*Charminus aethiopicus* (Caporiacco 1939) NEW COMBINATION. *Cispius novus* Caporiacco 1941 and *Cispius tertali* Caporiacco 1941 are both subjective junior synonyms of *Charminus aethiopicus* (Caporiacco 1939) NEW SYNONYMIES. The



male palps of *C. tertali* (♂ holotype) and *C. aethiopicus* (♂ syntypes) are morphologically identical. The female specimens of *Cispius novus* (♀ syntypes) share a unique somatic feature with *Cispius aethiopicus* and *Cispius tertali*: In all specimens, the outermost of the three cheliceral teeth at the retromargin is distinctly smaller than the other two (see cheliceral teeth in *Charminus camerunensis* for comparison). The female specimens of *Cispius novus* were collected at the same locality as the *Cispius tertali* specimen.

**Specimens examined.**—*Charminus aethiopicus*: **KENYA**: Moyale, 2♂ (syntypes), 18 May 1937 (MZUF). *C. ambiguus concolor*: **TANZANIA**: Arusha, 1♀, 1905 (HNHM). Moschi, 2♀, 1904 (HNHM). *C. ambiguus*: **SOUTH AFRICA**: Natal, St. Lucia National Park, Fanies Camp, 28°S, 32°30'E, 1♂2♀, 24 January 1991 (V.D. & B. Roth) (CASC). **MALAWI**: Mukuwazi, Hill Forest, 11 mi S of Nkata Bay, 590 m, 1♂, 22 February 1958 (E.S. Ross & R.E. Leech) (CASC). *C. camerunensis*: **CAMEROON**: Kitta, 5♂1♀ syntypes (NHRS 1406). **GABON**: Makokou, 2♀ (Riechert). *C. minor*: **ZAIRE**: Faradje III, 1♀, one of two syntypes [other syntype in MHNG, local 38] (AMNH). **NI-GERIA**: Ikeja Airport, Lagos, 1♀, 19 December 1948 (E.S. Ross & R.E. Leech) (CASC). *C. marfieldi*: **RUANDA**: 40 km E of Kigale, 1575 m, 1♀, 9 December 1957 (E.S. Ross & R.E. Leech) (CASC). *C. natalensis*: **ZAIRE**: 8 mi W of Luanxa, 1330 m, 1♀, 15 January 1958 (E.S. Ross & R.E. Leech) (CASC). *C. novus*: **ETHIOPIA**: El Banno, 3♀ (syntypes), 30 April–4 May 1939, Missione Biologica Sagan-Omo (Prof. E. Zavattari) (MZUF). *C. tertali*: **ETHIOPIA**: El Banno, 1♂ (holotype), 7 May 1939, Missione Biologica Sagan-Omo (Prof. E. Zavattari) (MZUF).

### *Cispius* Simon 1898

Figs. 6, 7, 12–16

*Cispius* Simon 1898a: 296. Type species, by original designation, *Cispius variegatus* Simon 1898b: 19, ♀, Congo, Landana.

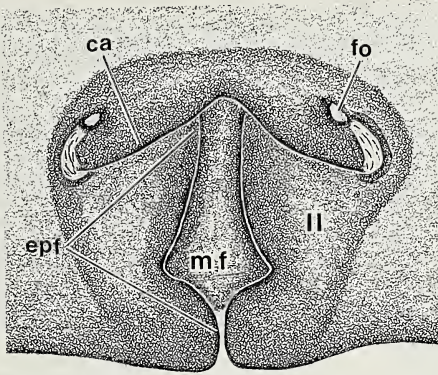
The genus currently contains eight species; four species are known from females only, three from males only. For *Cispius maruanus* both sexes are known (Blandin 1978a). Valid species of genus: *C. affinis* Lessert 1916, ♀ known; *C. bidentatus* Lessert 1936, ♂ known; *C. kimbius* Blandin 1978 (1978a), ♀ known; *Nilus maruanus* Roewer 1955, ♂ ♀ known; *C. problematicus* Blandin 1978 (1978a), ♂ known; *C. simoni* Lessert 1915, ♀ known; *C.*

*thorelli* Blandin 1978 (1978a), ♂ known; *C. variegatus* Simon 1898 (1898b), ♀ known.

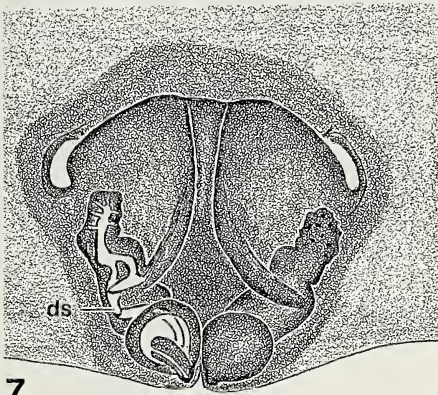
**Diagnosis.**—AE distinctly smaller than PE (ch 3), AER recurved (ch 2), three cheliceral teeth in most species (ch 0), epigynal folds anteriorly parallel and close to each other (ch 7), carina procurved (ch 9); conductor broad, rounded, flaplike (ch 22–25). Autapomorphic characters: Male retrolateral tibial apophysis large, broad and perpendicular; distal tegular apophysis large, with smoothly rounded apical margin, shape unique; distal sclerotized tube of embolic division large (ch 32), tip reaches tip of embolus, additional sclerite of species-typical size within pars pendula (ch 34), embolus short but massive (ch 33). Synapomorphic characters: Procurved carina as in *Charminus* (ch 9).

**Description of species.**—Measurements: *C. variegatus*, 3♀: Prosoma 2.4–2.9 long, 2.0–2.4 wide, body 5.0–7.1 long (MRAC 12.320/22). *C. thorelli*, 2♂ holotype, paratype: Prosoma 3.5–4.2 long, 2.9–3.4 wide, body 6.5–7.5 long (MRAC 121.176; 148.599). *C. bidentatus* ♂ holotype: Prosoma 6.9 long, 4.2 wide, body 11 long (MHNG, boc 38); ♂ prosoma 3.8 long, 3 wide, body 8 (MRAC 145.399). Eye pattern: AER recurved (sometimes almost straight) and only slightly shorter than PER, AE distinctly smaller than PE, PME:AME = 1.4; AME:ALE = 1.3. Chelicerae: *C. thorelli*, *C. variegatus*, and *C. problematicus*: Three teeth at posterior margin of chelicerae, outermost slightly smaller, *C. bidentatus* with only two (specimen from Tanzania with three cheliceral teeth); teeth unequal in size. Spine pattern and spine length: As in *Charminus*. Epigynum (*C. variegatus*, Fig. 6): Epigynal folds anteriorly parallel, small distance apart; entire carina procurved, posterior edge ridgelike, anterior edge weakly developed; fossae lateral to copulatory openings. Vulva (Fig. 7): Copulatory duct sclerotized, short and curved; large head of spermatheca pointing anteriorly, spermathecal duct with one loop, base of spermatheca large and bulbous with large lumen. Male palp (*C. thorelli*, Figs. 12–14): Retrolateral tibial apophysis large and perpendicular to tibia; conductor large with rounded tip; median apophysis slender with S-shaped hook; distal tegular apophysis with large, rounded tip; sclerite A similar to *Charminus*, distal tegular apophysis large, reaches tip of embolus; em-





6



7

Figures 6, 7.—*Cispius variegatus* from Zaire (MRAC 12.320). 6, Epigynum; 7, Vulva. Scale line = 0.5 mm.

bolus moderately long, but massive, pars pendula reaches tip of embolus; sclerite within pars pendula may represent truncus. *C. problematicus* (♀ unknown): ♂ with uniquely large sclerite A (see Blandin 1978a: fig. 21) and with two pointed sclerites visible at tip of the embolus as in *C. bidentatus*.

**Taxonomic notes.**—The species *Cispius orientalis* described by Yaginuma (1967) has been placed in a new genus *Shinobius* Yaginuma 1991. It has no affinities to the Pisaurinae, but to the Rhoicininae (Sierwald 1993). The types of *C. delesserti* Caporiacco 1947, *C. kovacs* Caporiacco 1947, and *C. strandi* Caporiacco 1947, cannot be located in the Museum in Budapest, Hungary (Mahunka *in litt.* 1986).

**Specimens examined.**—*C. bidentatus*: **MOZAMBIQUE**: Vila Pery, ♂ holotype (P. Lesne) (MHNG, bocal 38). **KENYA**: Diani Beach, 1♂, May 1957 (N.L.H. Kraus) (AMNH). **ZAIRE**: Al-

bertville, Verhonstraete, 1♂, 1960 (MRAC 145.399). **TANZANIA**: 10 mi SE of Amani, 160 m, 1♂, 11 November 1957 (E.S. Ross & R.E. Leech) (CASC). *C. kimbius*: **SOUTH AFRICA**: Natal, St. Lucia National Park, collected from hole in tree bark, Fannies Camp, 28°S, 32°30'E, 3♀, 24 January 1991 (V.D. & B. Roth) (CASC). *C. thorelli*: **ZAIRE**: Katanga, Elisabethville, ♂ holotype, January 1962 (M. Lips) (MRAC 121.176). Albertville, Verhonstraete, ♂ paratype, 1960 (MRAC 148.599). *C. problematicus*: **SOUTH AFRICA**: East Transvaal, 15 km from Klaserie, woodland, Guernsey Farm, 2♂, 18–31 December 1985 (S. & J. Peck) (AMNH). East Transvaal, stream side thorn scrub, Kruger Park, Satara, 1♂, 15–18 December 1985 (S. & J. Peck) (AMNH). *C. variegatus*: **ZAIRE**: Komi, Lodja, 3♀, January–February 1930 (MRAC 12.320–12.322).

#### *Afropisaura* Blandin 1976

Figs. 17–22, 25, 26

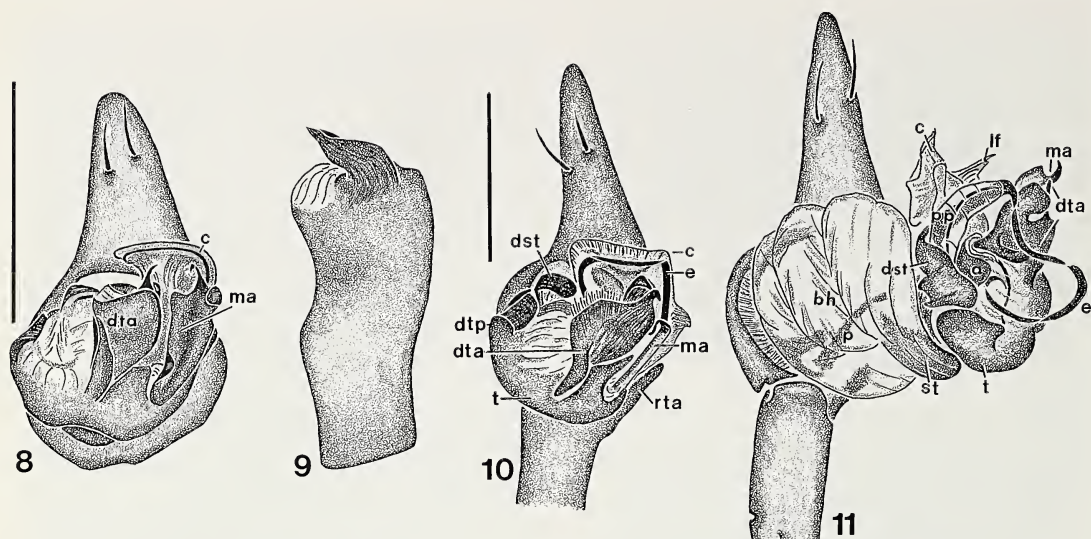
*Afropisaura* Blandin 1976b: 926. Type species, by original designation, *Pisaura valida* Simon 1885: 354 (♀), Senegal, Dakar.

Blandin (1976b) included *A. valida*, *A. rothiformis* (Strand 1908) and *A. ducis* (Strand 1913) in his newly described genus *Afropisaura* and placed *Pisaura camerunensis* Roewer 1955 in the synonymy of *A. ducis*. Both sexes are known for the three species.

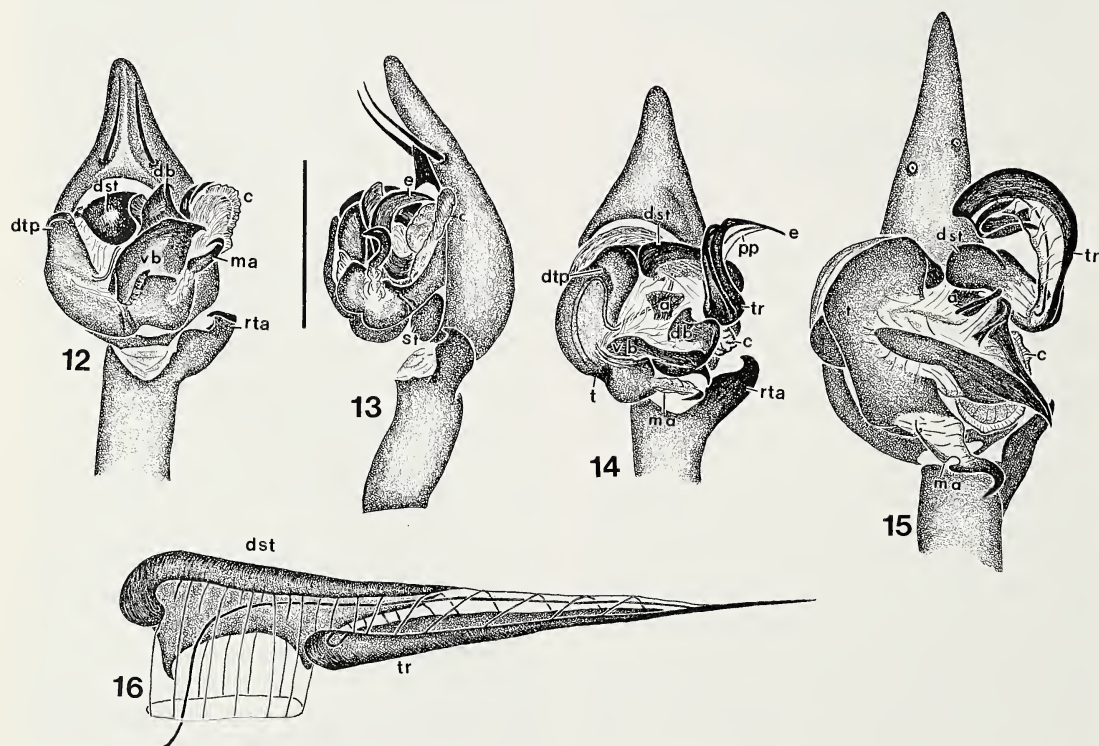
**Diagnosis.**—AER straight or slightly procurved (*ch* 2), ALE ≥ AME (*ch* 4); three equally-sized cheliceral teeth (*ch* 0), posterior section of copulatory duct of vulva with several, partly sclerotized undulations (*ch* 13). Autapomorphic characters: Truncus attached to distal sclerotized tube of embolic division, forming an angle; large median apophysis with blade-shaped tip; short conductor with broad base, tapering apically (*ch* 22). Central excavation opening posteriorly under lip-like carina. Vulva: Anterior section of copulatory duct sclerotized (*ch* 13). Synapomorphic characters: Liplike carina (*ch* 10), sclerotized anterior section of copulatory duct, and posterior section of copulatory duct undulated as in *Tetragonophthalma* (*ch* 13).

**Description of *A. valida* and *A. ducis*.**—Measurements: *A. ducis*: Both sexes of same size, males with longer legs than females. Female range from body 9.75 long [prosoma 3.5 long, 3.0 wide (SMFD RII/7930/52)] to body 13.49 long [prosoma 5.16 long, 4.33 wide (SMFD RII/10008)]. Male range from body 11.6 long [prosoma 4.58 long, 3.70 wide (ho-



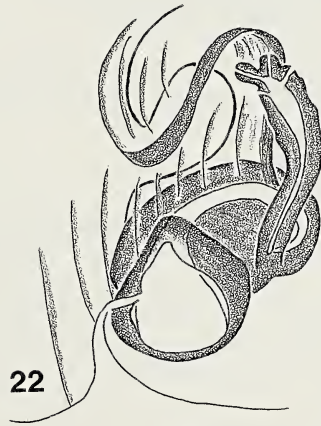
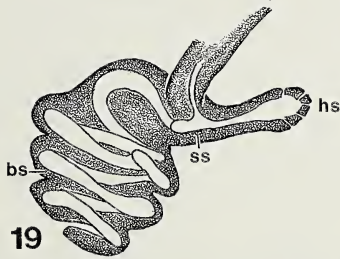
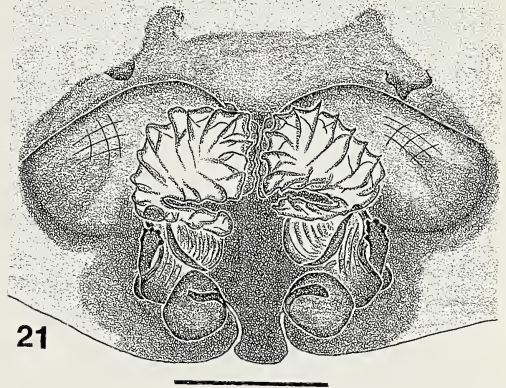
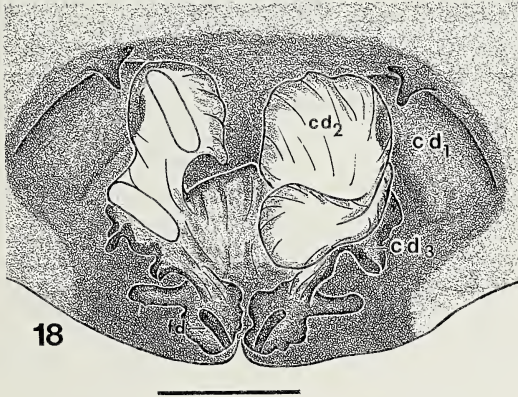
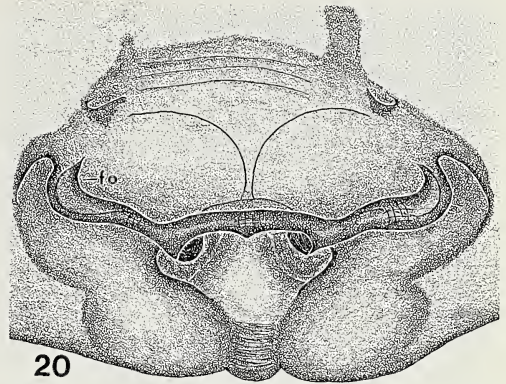
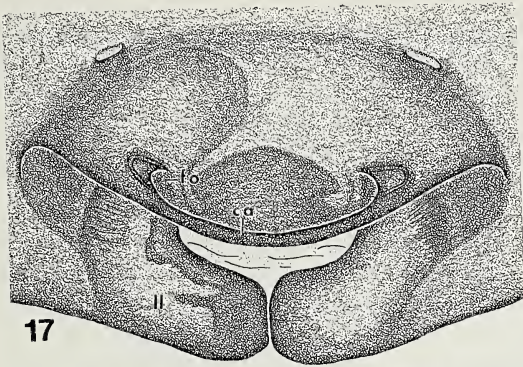


Figures 8–11.—*Charminus*, left male palp. 8, 9, *Charminus aethiopicus* from Kenya (syntype; MZUF). 8, Unexpanded palp, ventral view; 9, retrolateral tibial apophysis. Scale line = 0.5 mm. 10, 11, *Charminus camerunensis* from Cameroon (syntype; NHRS, 1406). 10, Unexpanded palp, ventral view; 11, Expanded palp, prolateral view. Scale line = 0.5 mm.



Figures 12–16.—*Cispius*, left male palp. 12–14, *Cispius thorelli* from Zaire (MRAC 148.599). 12, Unexpanded palp, ventral view; 13, Unexpanded palp, retrolateral view; 14, Expanded palp, ventral view (MRAC 148.599). 15, 16, *Cispius bidentatus* from Zaire (MRAC 145.399). 15, Expanded palp, ventral view; 16, Embolus sclerites, schematic. Scale line = 0.5 mm.





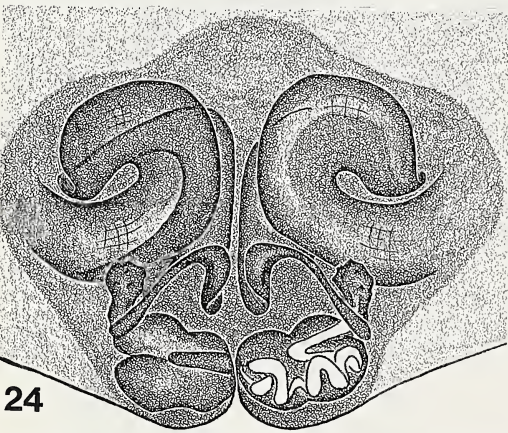
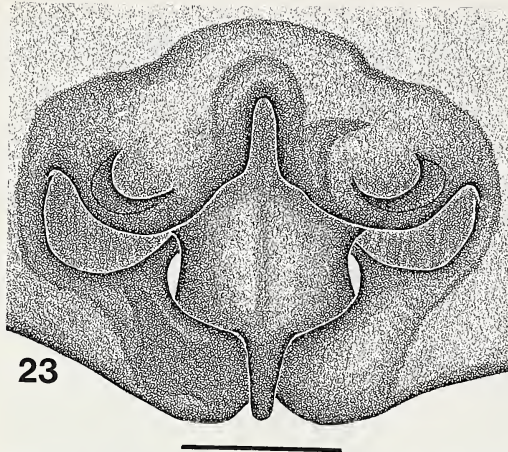
Figures 17–19.—*Afropisaura valida* from Congo (MRAC 29.531). 17, Epigynum; 18, Vulva; 19, Left spermatheca, dorsal view. Scale line: 17, 18 = 0.5 mm; 19 = 0.2 mm.

Figures 20–22.—*Afropisaura ducis* from Zaire (SMF RII/10008). 20, Epigynum; 21, Vulva; 22, Left spermatheca, dorsal view. Scale line: 20, 21 = 0.5 mm; 22 = 0.2 mm.

lotype *ducis*) to body 13.1 long [prosoma 5.2 long, 4.16 wide (SMFD RII/10329/79)]. *A. valida*: ♀ range from body 9.3 long [prosoma 4.16 long, 3.66 wide (MRAC 29 528-31)] to body 17 long [prosoma 7.08 long, 6.25 wide (lectotype, MNHN 4922)]. Leg length: (prosoma 4.16 long) Fe 4.41, PaTi 5.6, MeTa 5.41; total length 15.42. Male range from body 11.26 long [prosoma 4.66 long, 3.83 wide (MRAC 29647)] to body 12.88 long [prosoma 5.8 long, 4.5 wide (MNHN “néallotype”)]. Leg length (prosoma 4.66 long) Fe 5.83, PaTi 7.5, MeTa 7.16; total length 20.5. Eye pattern:

AER: Straight in *A. valida*, procurved in *A. ducis*; PME>PLE=ALE≥AME (*ch* 3,4), *A. valida*: PME:AME = 1.2, AME=ALE; *A. ducis*: PME:AME = 1.6, AME:ALE = 0.7; in *A. ducis* and *A. rothiformis* AME conspicuously smaller (Blandin 1976b, figs. 4, 19, 20)





Figures 23, 24.—*Tetragnophthalma vulpina* from Zaire (MRAC 12.668). 23, Epigynum; 24, Vulva. Scale line = 0.5 mm.

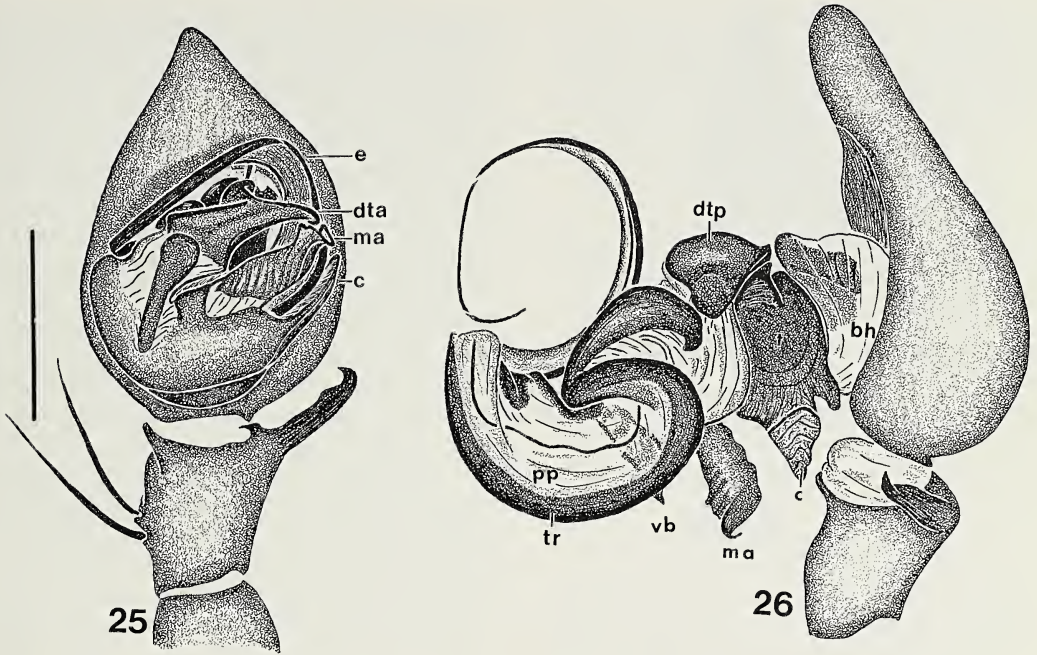
than in *A. valida*. Chelicerae: Posterior margin with three equally-sized teeth, equally spaced. Spine pattern (Table 6): Patella with a thin dorsal proximal spine and two lateral spines. Spine length [ventral tibial spine, second pair, first leg]: Spine length:tibia width = 3. Epigynum (Figs. 17, 20): Rather large in all three species; epigynal folds form a V; fossae above copulatory openings and in *A. valida* closer together than in *A. ducis*; deep pit under median section of carina opening posteriorly; copulatory openings in *A. valida* considerably larger than in *A. ducis*. Vulva (Figs. 18, 19, 21, 22): Copulatory duct divided in three sections; anterior section (cd1) sclerotized with large lumen; middle section (cd2) membranous saccate tube, forms two loops of unequal size; posterior section (cd3) narrow fold with sclerotized edge; head of spermatheca of mod-

erate size, pores conspicuous; position of head of spermatheca appears to be variable within *A. ducis* pointing anteriorly or posteriorly (type of *Pisaura camerunensis* [= *A. ducis*]; Head of spermatheca seems to point posteriorly, visible through body wall); *A. valida*—specimen examined: Head of spermatheca points laterally. *A. valida* (Fig. 19): Spermathecal duct with four loops; base of spermatheca without lumen. *A. ducis* (Fig. 22): Spermathecal duct forms single curve, base of spermatheca with large lumen. Male palp (Figs. 25, 26, based on *A. valida* and *A. ducis*, Blandin 1976b, fig. 26): Tegulum platelike and strongly sclerotized on both sides; conductor stiff, sclerotized, with broad base and pointed tip, considerably shorter than in all other Pisaurinae; prolateral wall of conductor membranous and inflatable; median apophysis flat with bladelike tip, pointing retrolaterally; distal tegular apophysis large, with club-shaped base, ventral branch ends in pointed hook. Sclerite A well developed with two prongs pointing dorsally in *A. valida*, simple saber-shaped in *A. ducis* (not visible in unexpanded palps). Distal sclerotized tube of embolic division large; truncus of embolus arises at its distal tip and runs backwards, thus forming a sharp angle (called “protuberance” by Blandin). Broad pars pendula follows truncus about  $\frac{3}{4}$  of embolus length; concave edge of pars pendula sclerotized, especially proximally.

**Natural history.**—Females of *Afropisaura valida* construct a nursery web (Blandin 1979b).

**Specimens examined.**—*A. ducis*: **ZAIRE**: Kivu Province, Lake Kivu, ♂ holotype, (ZMHB 28 356). **TANZANIA**: Arusha, ♀ “allotype” 2♂ (SMFD RII/10329/79). **ZAIRE**: Upemba Nat. Park, 1♂1♀ (SMFD RII/10008). **CAMEROON**: Yaoundé, 1♀ (holotype *Pisaura camerunensis*) (SMFD RII/7930/52). *A. rothiformis*: **NIGERIA**: Abarka (Kwale) Warri, 1♀, 2 January 1949 (B. Malkin) (CASC). **CAMEROON**: Mkuika, Victoria Div., 1♂, 24–29 June 1949 (B. Malkin) (CASC). **ANGOLA**: Lunda Province, Dundo, 1♀, 21 September 1949 (B. Malkin) (CASC). *A. valida*: **CONGO**: 1♂2♀, (MRAC 29.528-29.531). 1♂ (MRAC 29.647). **IVORY COAST**: Lamto, ♂ “néallotype” (MNHN). **SENEGAL**, ♀ lectotype (designated by Blandin) 2 juv. (MNHN 4.922). **ANGOLA**: Lunda Province, Dundo, 1♂, 21 September 1949 (B. Malkin) (CASC).





Figures 25, 26.—*Afropisaura valida*, left male palp from Congo (MRAC 29.647). 25, Unexpanded, ventral view; 26, Expanded, retrolateral view. Scale line = 1 mm.

*Tetragonophthalma* Karsch 1878

Figs. 23, 24, 27–30

*Tetragonophthalma* Karsch 1878: 329. Type species, by monotypy, *Tetragonophthalma phylla* Karsch 1878: 329; ♀ juvenile; Ghana, Accra. Immature female type specimen, apparently lost (*vide* Blandin 1976a: 588). Considered a *nomen dubium* by Blandin (1976a: 588).

Blandin (1976a) recognized eight valid species in the genus, placed *T. ferox* (Pocock 1899) in the synonymy of *T. crassa* (Thorell 1899), and listed five *nomina dubia*. Types of every available African species of the genus *Tetragonophthalma* (9♂12♀) were examined for the present study. All eight species are here considered to be conspecific. No concordant differences were found in the males examined. The female epigynum displays a moderate range of variation, but the vulvae display only minor variability. The body-length variation of adult females is high. Therefore, the nominal species *T. balsaci*, *Phalaea crassa*, *Phalaea ferox*, *T. guentheri*, *T. lecordieri*, *T. pelengeae*, *Phalaea thomensis*, and *T. wittei* are here regarded as subjective junior synonyms of *Tetragonophthalma vulpina* (Simon 1898). *Diapontia freiburgensis* Keyserling 1877 (1877: 671), transferred to

*Tetragonophthalma* by Keyserling (1891: 255), and *Tetragonophthalma obscura* Keyserling 1891 (1891: 256), the only South American species ever associated with one of the pisaurine genera as here defined, were transferred to *Porrimosa* Roewer 1960, family Lycosidae, by Capocasa (1982: 146).

*Tetragonophthalma vulpina* (Simon 1898)

*Phalaea vulpina* Simon 1898b: 14 (♂♀).

*Phalaea crassa* Thorell 1899: 80 (♀) NEW SYNONYMY.

*Phalaea ferox* Pocock 1899: 863 (♀); considered a subjective junior synonym of *crassa* by Blandin (1976a: 592) NEW SYNONYMY.

*Phalaea thomensis* Simon 1909: 386 (♀) NEW SYNONYMY.

*T. guentheri* Roewer 1955: 172 (♀) NEW SYNONYMY.

*T. pelengeae* Roewer 1955: 179 (♂♀) NEW SYNONYMY.

*T. wittei* Roewer 1955: 181 (♂♀) NEW SYNONYMY.

*T. lecordieri* Blandin 1976a: 601 (♂♀) NEW SYNONYMY.

*T. balsaci* Blandin 1976a: 602 (♂♀) NEW SYNONYMY.

**Diagnosis.**—Large spiders (♀ up to 40 mm long) with the following autapomorphic char-

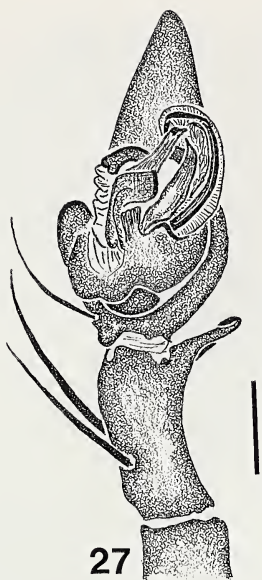
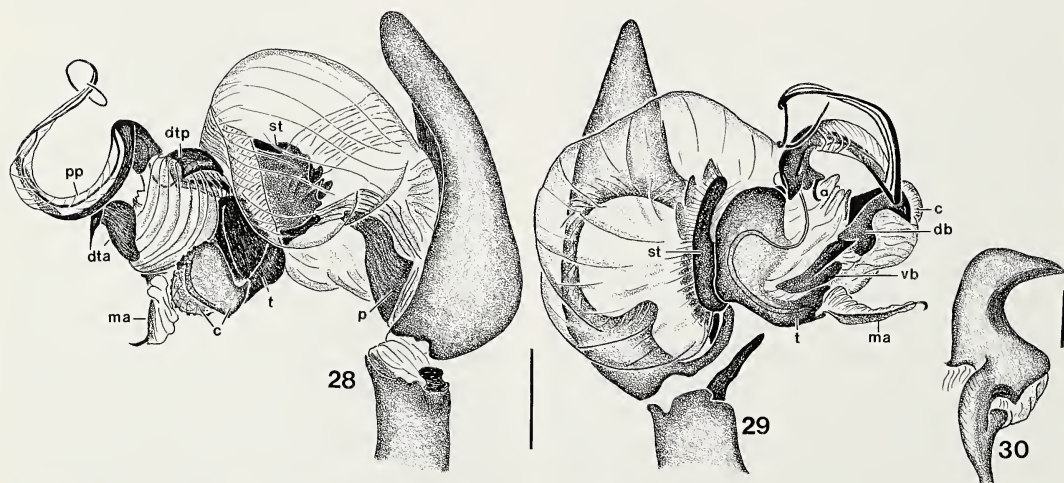


Figure 27.—*Tetragnophthalma vulpina*, left male palp, unexpanded, ventral view; (paratype of *T. lecordieri*; MRAC 123.720). Scale line = 1 mm.

acters: AER strongly procurved (*ch* 2); four cheliceral equally-sized teeth (*ch* 0, 1); sexual dimorphism in spination of patella and tibia unique within the Pisaurinae (*ch* 5); spines short (*ch* 6); carina continuous, with deep median notch; copulatory duct fully sclerotized (*ch* 13); hook at distal tegular apophysis in male bulb large. Synapomorphic characters:

Liplike carina (*ch* 10), sclerotized anterior section of copulatory duct and undulated posterior copulatory duct shared with *Afropisaura* (*ch* 13).

**Description of *T. vulpina*.**—Measurements: Females are larger than males, males have relatively longer legs than females. Female body range from 16.1 long (prosoma 6.8 long, 5.2 wide [holotype of *P. thomensis*]) to 40 long (prosoma 16 long, 11.4 wide [holotype of *P. crassa*]). Leg length: Female (prosoma 8.4 long, holotype of *T. lecordieri*) Fe 13.5, PaTi 18.3, MeTa 22; total length 53.8. Male body range from 16.7 long (prosoma 6.2 long, 5 wide [paratype of *T. lecordieri*]) to 24.5 long (prosoma 10 long, 8.4 wide [paratype of *T. pelengeae*, MRAC 119.706]). Leg length (prosoma 8.2 long, [paratype of *T. pelengeae*, MRAC 119.706]) Fe 17, PaTi 22, MeTa 24; total length 63. Eye pattern: AER strongly procurved; anterior lateral eyes on tubercles of variable size; PLE > PME = ALE > AME (*ch* 3,4); PME:AME = 1.1–1.48. AME:ALE = 0.7–0.9. Variability in eye-sizes reflects variability in body-size. Chelicerae: Posterior margin typically with four equally-sized teeth. Variation: Less than four teeth on one chelicera or small additional tooth or teeth of different sizes, e.g., *P. thomensis*: Right chelicera 3, left chelicera 4. Spine pattern (see Table 6): Patella spination on legs I and II differs from patella spination on legs III and



Figures 28–30.—*Tetragnophthalma vulpina*, expanded left male palp. 28, 29, Ivory Coast (paratype of *T. lecordieri*; MRAC 123.720); 30, Congo (paratype of *T. balsaci*, MNHN, Simon coll 8536). 28, Expanded, retrolateral view; note expanded conductor; 29, Expanded, ventral view; 30, Hook at distal tegular apophysis, prolateral view. Scale line: 28, 29 = 1 mm; 30 = 0.2 mm.



IV. Sexual dimorphism in dorsal spination of tibia I and II. Spine length: Short [ventral tibial spine, second pair, first leg]: Spine length: tibia width = 1.5. Epigynum (Fig. 23): Epigynal folds anteriorly divergent, middle section straight and far apart, posterior section adjoining; carina continuous, unique shape, forming two flaps over copulatory openings; fossae approximately above copulatory openings. Vulva (Fig. 24): Copulatory duct entirely sclerotized, with two wide loops and a narrow posterior section; head of spermatheca pointing anteriorly, spermathecal duct with five loops, base of spermatheca without lumen. Male palp (Figs. 27–30): Retrolateral tibial apophysis simple, perpendicular to palpal tibia; conductor large, tip broad with low guiding fold; median apophysis slender with hook; distal tegular apophysis with hook, without wing; sclerite A small, rod-shaped; embolus moderately long, pars pendula over  $\frac{2}{3}$  of embolus.

**Natural history.**—Pocock (1899) mentioned a collector's description of a "*Tetragonophthalma phylla*" web. That description fits the figure given by Blandin (Blandin & Celerier 1981) for webs of the genus *Euprosphenops*. Blandin (1976a) collected *Tetragonophthalma* in wooded habitats. According to my own observations (1980, South Africa, Natal, Hluhluwe) *Tetragonophthalma* lives arboreally and does not build webs.

**Specimens examined.**—**CONGO:** ♂ paratype of *T. balsaci*, (ES 8536) [ex syntype of *T. vulpina*] (MNHN). **CAMEROON:** ♀ holotype of *T. crassa* (Sjöstedt leg. 1891) (NHRS 1403). **EQUATORIAL GUINEA:** *Benito-River*, ♀ holotype of *T. ferox* (BMNH 1898.5.5 101-102) (part). Blandin (1976a: 592) noted three syntypes of *ferox*; Pocock (1899: 863) described ♀ (♀ holotype in BMNH). **TOGO:** ♀ holotype of *T. guentheri* [Parts of ♀ holotype mounted on microscope slides, vial contains remaining parts of holotype and another adult ♀] (ZMHB 13832). **IVORY COAST:** *Lamto*, ♀ holotype of *T. lecordieri* (ENS) (MNHN); *Lamto*, ♀ paratype [cited in Blandin (1976a) with incorrect collection number] (MRAC 134.609); *Bingerville*, ♂ paratype (MRAC 123.720). **ZAIRE:** *Luebo*, ♀ [marked on vial as paratype, not listed as paratype in Blandin 1976a] (MRAC 12.668). **ISL. S. THOMÉ:** *Ribera Palma*, ♀ holotype of *T. thomensis* (MCSN). **ZAIRE:** *Gorges de la Pelenge*, Upemba National Park, ♀ holotype of *T. pelengea* (MRAC 119.705); 2 ♂ paratypes (MRAC 119.706). *T. phylla* (det. Pocock): **SIERRA LEONE:** 1♂1♀

(BMNH 1898.5.5.95-100). **CONGO:** ♀ holotype of *T. vulpina*, (ES. 8536) (MNHN). **GABON:** 1♂ (AMNH). **ZAIRE:** *Mabwe*, Upemba National Park, ♂ holotype of *T. witte* (MRAC 119.707); ♀ paratype (MRAC 119.708).

*Perenethis* L. Koch 1878

Figs. 31–81

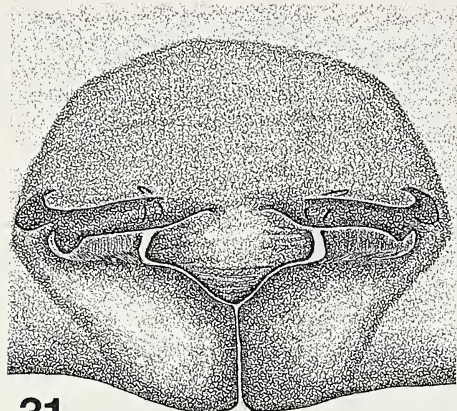
*Perenethis* L. Koch 1878: 980. Type species, by monotypy, *Perenethis venusta* L. Koch 1878: 980 (♀), Australia, Rockhampton.

Blandin (1975a) recognized four African species. For the present study, all available type material of African and Asian species was examined. Here, two African species (*P. simoni* and *P. symmetrica*), three Asian species, (*P. dentifasciata*, *P. fascigera*, and *P. sindica*), and one Australian species (*P. venusta*) are recognized. *Perenethis huberti* Blandin 1975 and *P. lejeuni* Blandin 1975 are considered subjective junior synonyms of *P. symmetrica* (see Sierwald 1989a).

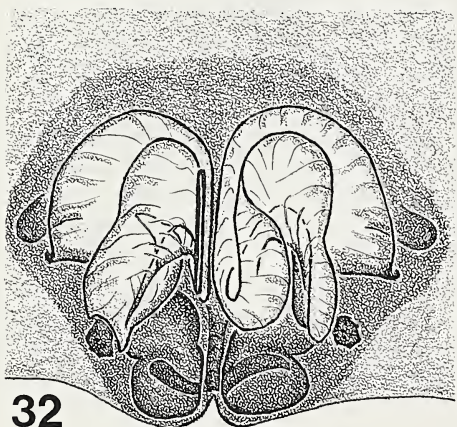
**Diagnosis.**—Two cheliceral teeth (*ch* 0), AER slightly procurved (*ch* 2), copulatory duct membranous and saccate (*ch* 13), forming two loops (*ch* 14), of which the first is wider than the second (*ch* 15), conductor with narrow base (*ch* 25), tegulum with basal protuberance (*ch* 21). Autapomorphic characters: Male palp with ventral tibial apophysis (*vta*, *ch* 20); conductor with small mesal hump (*ch* 26) and slender apical section with smoothly rounded tip (*ch* 24); carina forming two lateral branches (*ch* 8). Synapomorphic characters: Two cheliceral teeth at retromargin (*ch* 0) and tegulum with basal protuberance shared with *Polyboea* and *Maypaci* (*ch* 21).

**Description of characters.**—Eye pattern: AER mostly procurved in varying degrees; eyes rather small and subequal, PLE = PME > AME > ALE, PME:AME = 1.2; AME: ALE = 1.2. Chelicerae: Posterior margin with two unequally-sized teeth close to the inner part of the chelicerae. Color pattern: Median yellowish-brown, rarely red-brown; dorsal pattern with light lateral stripes along prosoma and opisthosoma enclose darker median sections; ventral pattern with grayish coloration of legs (especially femora), dark spots on coxae, grayish patches on sternum. Spine pattern: Legs as in *Charminus*, some specimens with thin, short pro- and retrolateral spines at the patella. Palpal femora with thin ventral spines, feature unusual in the Pisaurinae. Spine length

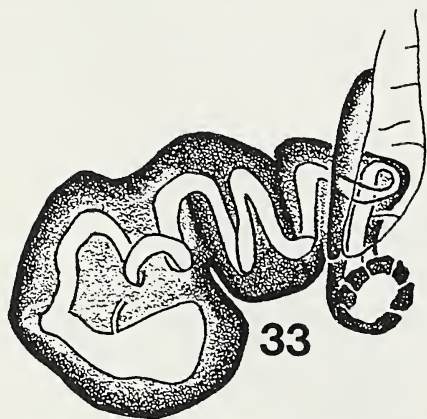




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32



33

Figures 31–33.—*Perenethis simoni* from Ivory Coast (MNHN). 31, Epigynum; 32, Vulva; 33, Left spermatheca, dorsal view. Scale line: 31, 32 = 0.5 mm; 33 = 0.2 mm.

[ventral tibial spine, second pair, first leg]: Spine length:tibia width = 3. Epigynum (Fig. 31): Epigynal folds V-shaped, carina ridge-like, straight (except in *P. symmetrica*), form-

ing two separate lateral branches; fossae located in the most lateral corners of the carina branches, lateral in relation to copulatory openings. Vulva (Fig. 32): Copulatory duct saccate and membranous forming two large loops, head of spermatheca bent except in *P. dentifasciata*, spermathecal duct with 3–6 loops, base of spermatheca with small or large lumen. Male palp (Figs. 54–81): Tibia with ventral apophysis; retrolateral tibial apophysis simple and flat, of various lengths, directed forward; tegulum with distinct basal protuberance; weakly sclerotized conductor with narrow base, distinct mesal hump (especially when inflated) and slender apical section with smoothly rounded tip; median apophysis with sclerotized hook; distal tegular apophysis with wing; sclerite A small, oval, elongated; distal sclerotized tube of embolic division short and small, consisting mainly of base; embolus long and whip-shaped, pars pendula about  $\frac{2}{3}$  of embolus length (except *P. symmetrica*).

**Natural history.**—Koh (1989) collected *P. venusta* in Singapore in “grassy areas”; label indicates collecting with sweep-net. Blandin (1975a) collected *P. simoni* among herbaceous plants. Web-building unknown.

#### REVISION OF THE GENUS *PERENETHIS*

##### *Perenethis dentifasciata* (O. Pickard-Cambridge 1885)

Figs. 48–50

*Ocyale dentifasciata* O. Pickard-Cambridge 1885: 79; female holotype; type locality: North-east PAKISTAN or north-west INDIA (“Murree to Sind valley, and Sind valley”); OXUM; *vidi*.

*Pisaura dentifasciata*, –Simon 1898a: 289.

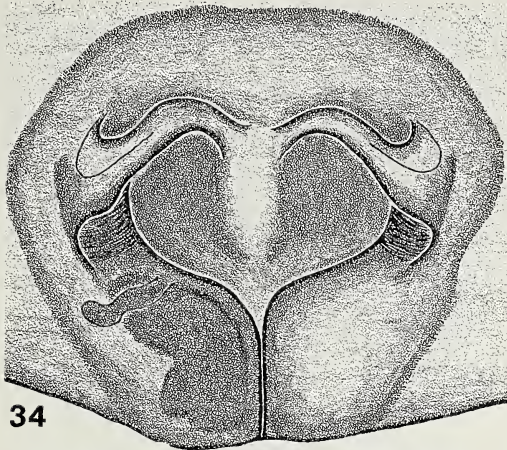
*Perenethis dentifasciata*, –Sierwald 1987a: 97.

Catalogs: Roewer 1954, 2a: 121, *sub Pisaura*. Bonnet 1955, 2: 3674, *sub Pisaura*. Platnick 1993: 520, *sub Perenethis*.

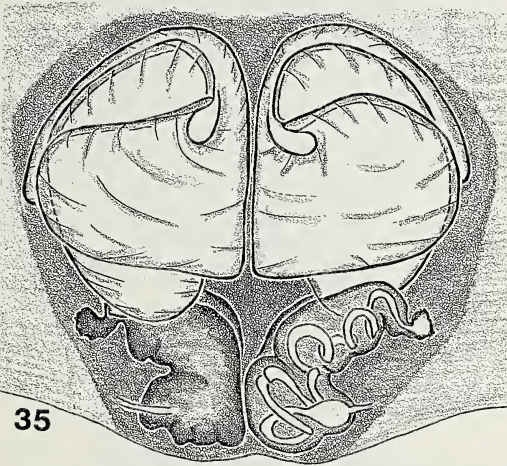
**Diagnosis.**—Carina branches very short, unique within *Perenethis* (Fig. 48).

**Description (only ♀ holotype known).**—Body, legs and palps light yellowish-brown; color pattern faded, most hairs lost; remnants of standard dorsal color pattern similar to *P. simoni* and *P. venusta* (Figs. 52, 53). Measurements: Body 10.6 long, prosoma 3.8 long, 3.25 wide. Leg length: Fe 4.66, PaTi 6.33, MeTa 6.75, total length 17.74. Epigynum (Fig. 48): Central transverse section of carina completely reduced, carina ridges only present around lateral epigynal pits. Vulva (Figs. 49,





34



35

Figures 34, 35.—*Perenethis symmetrica* from Djibouti (holotype of *Perenethis huberti*; MNHN). 34, Epigynum; 35, Vulva. Scale line = 0.2 mm.

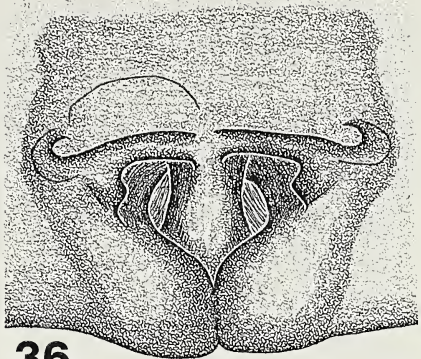
50): Copulatory duct saccate and membranous with two loops, first loop considerably wider; small head of spermatheca pointing anteriorly; spermathecal duct with three loops; base of spermatheca ball-shaped with large lumen. Male unknown, see under “Special Forms” for a possible male.

**Distribution.**—Known only from type locality.

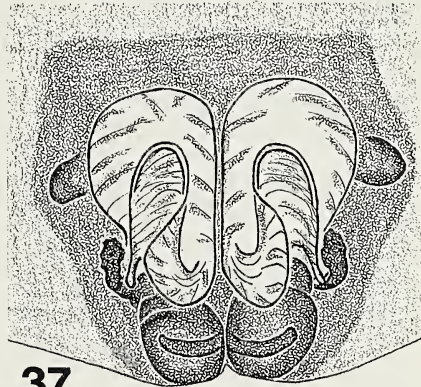
*Perenethis fascigera* (Bösenberg & Strand 1906)

*Tetragonophthalma fascigera* Bösenberg & Strand 1906: 306; female holotype; type locality: Japan; Naturkunde-Museum Stuttgart; *non vidi* (holotype lost).

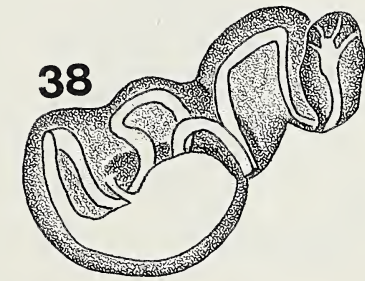
*Perenethis fascigera*, —Hu 1984: 260. Yaginuma 1986: 173 (♂ ♀). Song 1987: 209. Chikuni 1989:



36



37



38

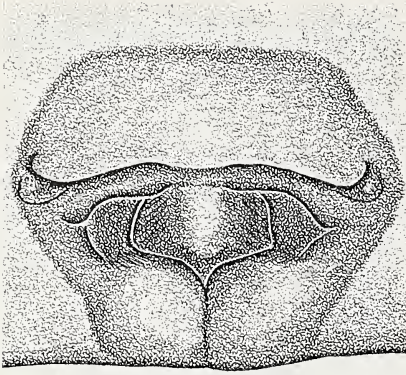
Figures 36–38.—*Perenethis sindica* from Nepal (CM 267, Mechi District, Taplejung). 36, Epigynum; 37, Vulva; 38, Left spermatheca, dorsal view. Scale line: 36, 37 = 0.5 mm; 38 = 0.2 mm.

106. Chen & Gao 1990: 136. Chen & Zhang 1991: 225.

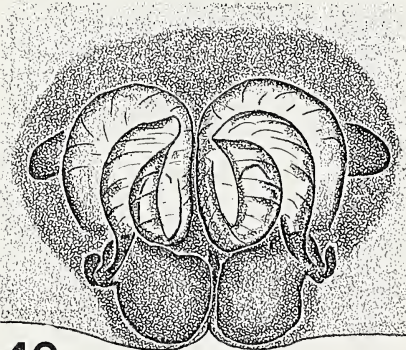
Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4360, *sub Tetragonophthalma*. Platnick 1989: 394, *sub Perenethis*; Platnick 1993: 520.

**Description.**—Single ♂ and single ♀ from Japan). *Female*: Body, legs and palps yellowish-brown, dorsal color pattern as in *P. venusta* (Fig. 53). Measurements: Body

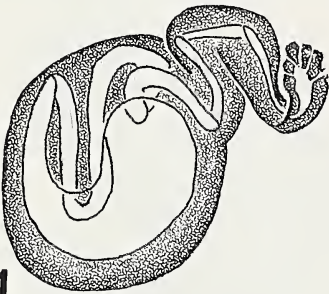




39



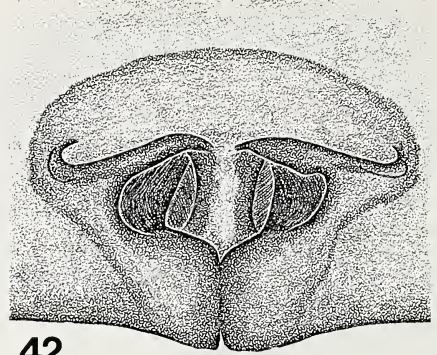
40



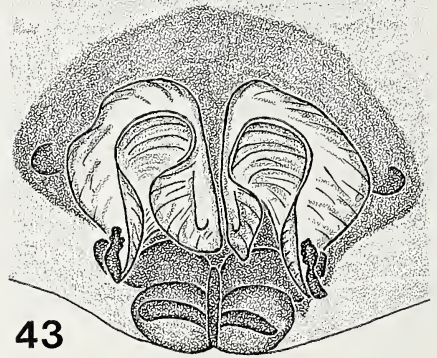
41

Figures 39–41.—*Perenethis sindica* from Sri Lanka (OXUM bottle 1526). 39, Epigynum; 40, Vulva; 41, Left spermatheca, dorsal view. Scale line: 39, 40 = 0.5 mm; 41 = 0.2 mm.

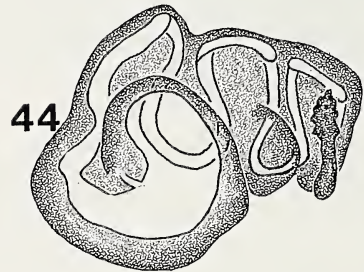
8.53 long, prosoma 3.41 long, 2.83 wide; legs all broken off. Epigynum: As in *P. sindica* (Figs. 36, 39). Vulva: As in *P. venusta* (Figs. 43, 46), spermathecal duct less convoluted than in *P. venusta*. Male: Coloration as in female, legs ventrally not dark-gray as in *P. venusta* but yellowish-brown. Measurements: Body 8.33 long, prosoma 3.32 long, 2.6 wide. Leg length: Fe 5.34, PaTi



42



43



44

Figures 42–44.—*Perenethis venusta* from Australia (lectotype, ZMUH). 42, Epigynum; 43, Vulva; 44, Left spermatheca, dorsal view. Scale line: 42, 43 = 0.5 mm; 44 = 0.2 mm.

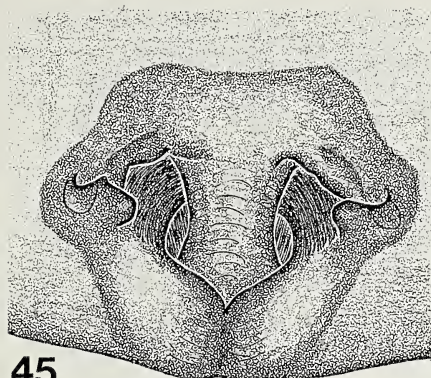
6.41, MeTa 8.34, total length 20.08. Leg formula: (I, II) IV, III, leg length differences small. Male palp very similar to *P. venusta* (Figs. 57), tibial apophysis short, distal tegular apophysis with wing.

**Remarks.**—*Perenethis fascigera* may be conspecific with *P. venusta*.

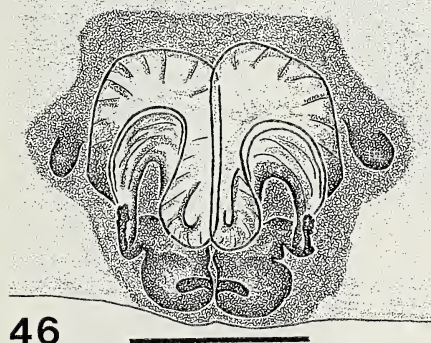
**Distribution.**—Known from Japan and China.

**Specimens examined.**—JAPAN: Kyushu, Ushibuka, ;1♂1♀, 29 July 1978 (Y. Chikuni). Loan: Courtesy of T. Yaginuma.

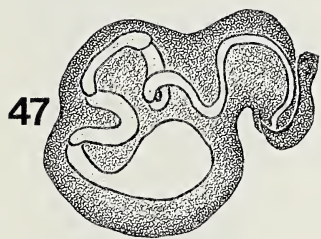




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Figures 45–47.—*Perenethis venusta* from Australia (paralectotype; MCSN). 45, Epigynum; 46, Vulva; 47, Left spermatheca, dorsal view. Scale line: 45, 46 = 0.5 mm; 47 = 0.2 mm.

*Perenethis simoni* (Lessert 1916)  
Figs. 31–33, 51, 52, 54–56)

? *Tetragonophthalma phylla*, –Simon 1898: 293, CONGO: Landana MNHN ES no. 3080; *non vidi* (listed by Blandin 1975a: 379).

*Tetragonophthalma simoni* Lessert 1916: 577; 2♂, 1♀ syntypes; type locality: ♀ lectotype [here designated], KENYA: Nanyuki [specimen label: Ngare na nyuki], Expedition Sjöstedt; NHRS; ♂ paralectotype [right palp missing], juvenile ♂ paralectotype, TANZANIA: Arusha, Kibonoto [presumably Kibongoto], Expedition Sjöstedt; NHRS; *vidi*.

*Maypacijs berlandi* Roewer 1955: 160, *nomen novum*; ♂ ♀ syntypes; type locality: ETHIOPIA: Barko; MNHN (det. by Berland as *Tetragonophthalma stuhlmanni*); *non vidi*. Synonymy by Blandin 1975a: 379.

*Perenethis straeleni* Roewer 1955: 265, ♂ holotype, type locality: ZAIRE, Upemba National Park, Mabwe, Lac Upemba; MRAC 119709; *non vidi*. Synonymy by Blandin 1975a.

*Perenethis simoni*, –Blandin 1975a: 379; 3♂3♀; IVORY COAST, Lamto, MNHN; *vidi*.

*Pisaurellus badicus*, –Blandin 1976b: 926, figs. 2, 7b, 8 [non *Pisaurellus badicus* Roewer 1961, see *Perenethis symmetrica* below].

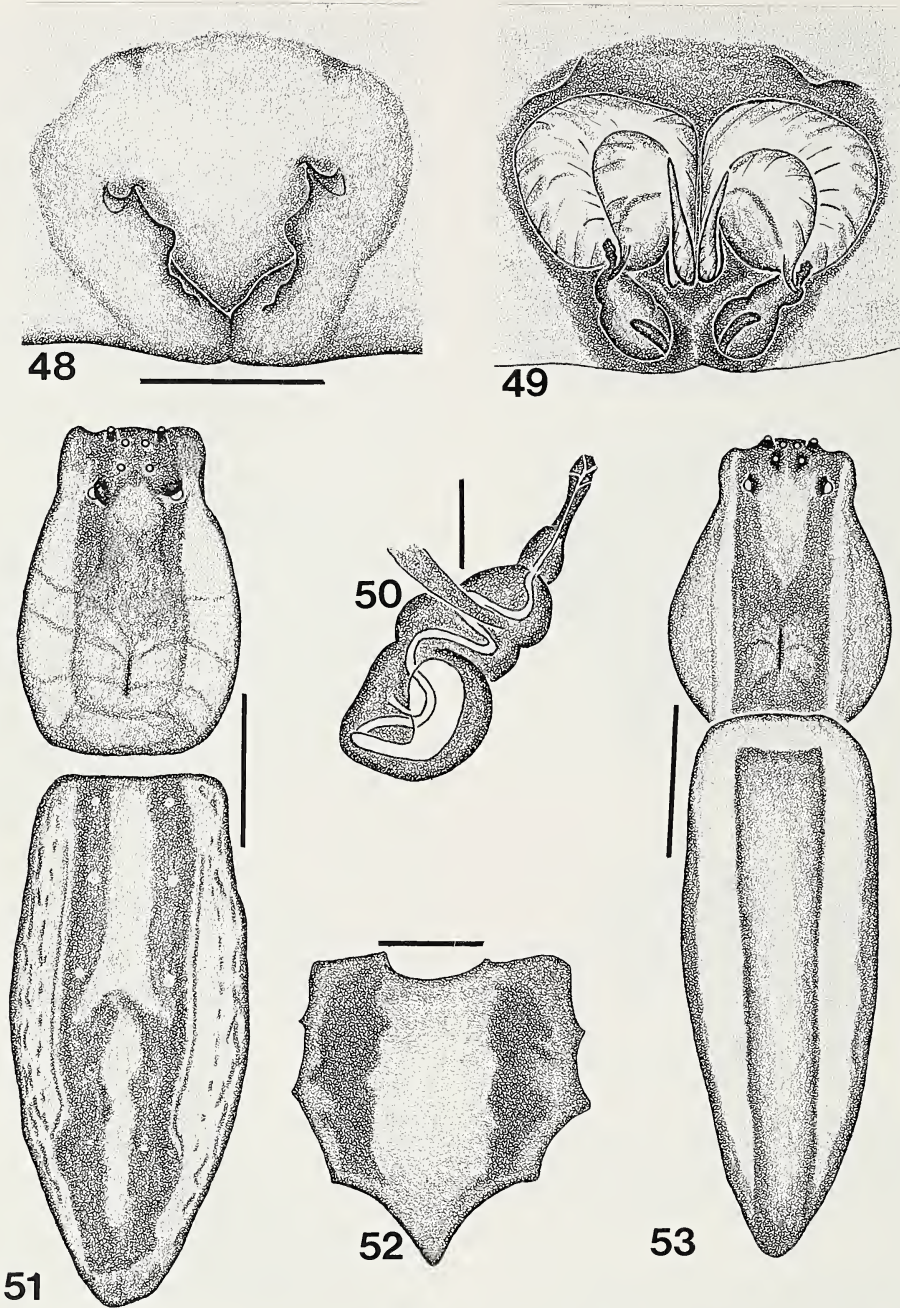
Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4361, *sub Tetragonophthalma*. Platnick 1993: 520.

**Note:** In the original description, Lessert (1916: 580) mentioned three specimens (collected in Kibonoto [2♂, not indicated as subadult] and Ngare na nyuki [1♀] during the Sjöstedt Expedition [1905–1906]). One adult male, one subadult male (labelled Kibonoto) and one female (labelled Ngare na nyuki) are deposited in the Naturhistoriska Riksmuseet in Stockholm. Female here designated as lectotype. A left male palp (from Kibonoto, MNHNG), labelled syntype, is not part of the adult male syntype from Stockholm (palp is too large). Blandin (1975a: 379) erroneously cited a female in MNHNG as holotype of *T. simoni* [specimen label states: ZAIRE: Garamba]. This female from Zaire, Garamba, was collected during the American Museum Congo-Expedition in 1937.

**Diagnosis.**—Epigynum with straight carina (*ch* 9); head of spermatheca bent dorsally pointing anteriorly (*ch* 16), first loop of spermathecal duct forming a complete circle; male conductor with fringed edge. *P. simoni* very similar to *P. sindica* and *P. venusta*, the latter two with fewer loops in the spermathecal duct. Coloration, structure of male and female copulatory organs similar to *P. venusta* and *P. sindica*.

**Description.**—*Female:* (7♀). General coloration of body, legs and palps yellowish-brown, prosoma with whitish lateral bands (Fig. 51); opisthosoma with light median band and two whitish stripes laterally; sternum with two dark lateral patches (Fig. 52). Legs ventrally grayish-black, especially the femora. Measurements (♀ lectotype): Body 10.9 long, prosoma 4.0 long, 3 wide. Largest female measured: Body 16 long,



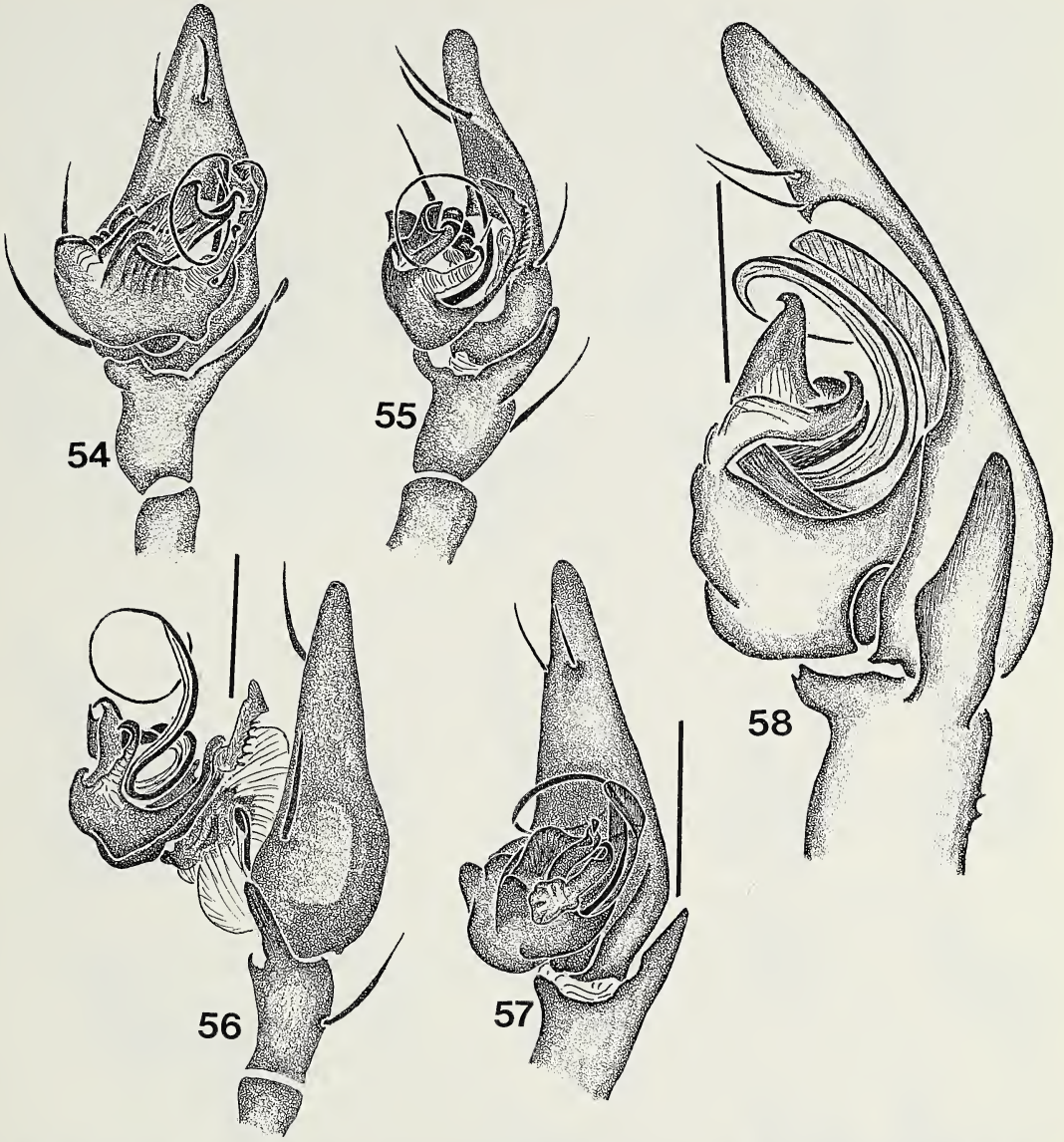


Figures 48–53.—*Perenethis*, female organs and color pattern. 48–50, *P. dentifasciata* from Pakistan or India? (Yarkand Mission, holotype; OXUM). 48, Epigynum; 49, Vulva, 50, Left spermatheca, dorsal view. 51–52.—*P. simoni* from Kenya (lectotype; NHRS): 51, Color pattern sternum; 52, Dorsal color pattern, female. 53, *P. venusta* from Australia, dorsal color pattern (female lectotype; ZMUH). Scale lines: 48, 49 = 0.5 mm; 50 = 0.1 mm; 51 = 1 mm; 52, 53 = 2 mm.

prosoma 4.4 long, 3.3 wide. Leg length (prosoma 4.0 long): Fe 6.4, PaTi 7.8, MeTa 9.166, total length 23.4. Epigynum (Fig. 31): Straight ridge-like carina conspicuous.

Vulva (Fig. 32): Copulatory duct saccate and membranous, forming two large loops, first loop slightly wider than second; head of spermatheca ball-shaped (Fig. 33), bent

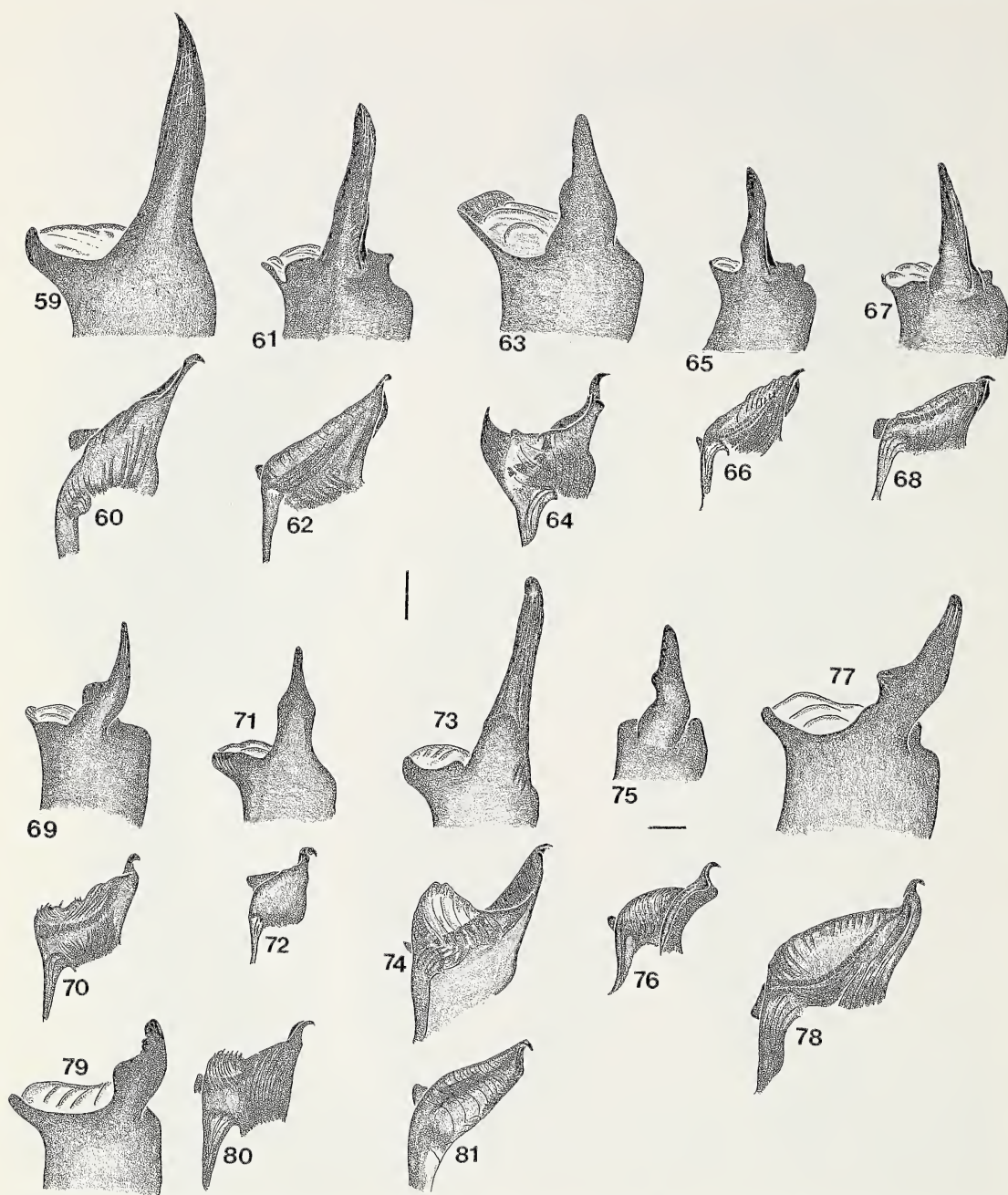




Figures 54–58.—Left male palp of *Perenethis*. 54–56, *P. simoni* from Ivory Coast (MNHN). 54, Unexpanded, ventral view; 55, Unexpanded, retrolateral view; 56, Expanded, retrolateral view. 57, *P. venusta* from Australia (MCSN), unexpanded, retrolateral view. 58, *P. symmetrica* from South Africa (AMNH), unexpanded, retrolateral view. Scale lines: 54–57 = 1 mm; 58 = 0.5 mm.

dorsally; stalk of spermathecae large and strongly sclerotized; spermathecal duct with five loops, the first loop describing a complete, small circle, the fourth loop tilted dorsally; base of spermatheca with small lumen. *Male*: (5♂). Coloration and pattern as in females. Measurements: Adult paralectotype: Body 15.16 long, prosoma 5.1 long, 3.75 wide. Smallest specimen: Body 11.2 long, prosoma 4.4 long, 3.5 wide. Leg

length (prosoma 4.1 long): Fe 7.0, PaTi 9.08, MeTa 11.6, total length 27.7. Male palp (Figs. 54–56): Retrolateral tibial apophysis long and flat (spatula-shaped), tip rounded; short hump-shaped ventral tibial apophysis, forming a projection of the apical tibial edge; median apophysis narrow, with terminal, sclerotized hook; distal tegular apophysis with terminal hook and conspicuous “wing”; conductor narrow, partly ex-



Figures 59-81.—Retrolateral tibial apophysis (odd numbers) and distal tegular apophysis (even numbers) of left male palp. 59-74, *Perenethis sindica*. 59, 60, From India: Bombay (OXUM bottle 1522); 61, 62, From India: Bombay (OXUM bottle 1525); 63, 64, From India: Kanchrapara (AMNH); 65, 66, From Sri Lanka (OXUM bottle 1526, tube A); 67, 68, From Sri Lanka (OXUM bottle 1526, tube B); 69, 70, From Nepal: Bagmati Dist., Kathmandu-Valley, Balaju Park, September 1969 (CM); 71, 72, From East Pakistan or northwest India (Yarkand Mission; OXUM). 73, 74, *P. simoni* from Ivory Coast (MNHN). 75, 76, *P. venusta* from Australia (note different scale line; MCSN). 77-80, *Perenethis* sp., special forms. 77, 78, From Turkey: Smyrna (OXUM); 79, 80, From Nepal: Dhading Dist, between Kagune and Samari Banjang, 800-1000 m, 23 July 83, agricultural area (CM). 81, *P. symmetrica* from South Africa (AMNH), distal tegular apophysis. Scale lines = 0.2 mm.



pandable, with fringed edge; embolus long, whiplike with pars pendula following  $\frac{2}{3}$  of embolus length. Leg formula ( $\delta$  ♀): (I-II), IV, III.

**Natural history.**—Occurs in savanna vegetation (Blandin 1975a: 380).

**Distribution.**—Africa, south of the Sahara.

**Specimens examined.**—Types listed above. **TANZANIA:** *Arusha*, Kibonoto, Expedition Sjöstedt, 1♂ (left palp only), MNHNG [labelled syntype]. **ZAIRE:** *Garamba* (det. Lessert), American Museum Congo-Expedition, ♀ labelled holotype by Blandin (MNHNG). **IVORY COAST:** *Lamto*, 3♂; 3♀ (MNHNG). **SENEGAL:** *Dakar*, km 15 R. Rufisque, 1♀, August 1980 (W. Settle) (CASC). **BOTSWANA:** *Serowe*, 1♀, *ex* malaise trap, March 1990 (P. Forchhammer) (CASC). **ZIMBABWE:** 33 mi SE of Chirundu, 1170 m elev., 1♂, 8 March 1958 (S. Ross & R.E. Leech) (CASC).

*Perenethis sindica* (Simon 1897)

Fig. 36–41, 59–72

*Tetragonophthalma sindica* Simon 1897: 295; 2♀ syntypes; type locality: INDIA [near Bombay] Kurrachee (MNHNG), *vidi*.

*Perenethis indica* [sic!], Pocock 1900: 246; ♀ (BMNH 99.11.2.147), *vidi*.

Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4361, *sub Tetragonophthalma*.

**Diagnosis.**—Female copulatory organ very similar to *P. simoni* and *P. venusta*, spermathecal duct with fewer loops than *P. simoni*. Male retrolateral tibial apophysis often pointed (*ch* 19).

**Description.**—Chelicerae: Inner tooth at posterior margin twice as large as outer tooth. *Female:* (17♀). Overall coloration yellowish-brown to medium brown; prosoma and opisthosoma dorsally with broad, dark, median band; set off by narrow, straight stripes of silver or white; sternum and opisthosoma ventrally with pale median band. Opisthosoma slender and elongated. Legs uniformly brown. Measurements: Range: Body 8.7 long, prosoma 3.3 long, 2.8 wide (Sri Lanka) to body 20.4 long, prosoma 5.8 long, 4.5 wide (INDIA: West Bengal). Leg length (prosoma 3.75 long): Fe 5.7, PaTi 7.1, MeTa 8.6, total length 21.5. Epigynum (Figs. 36, 39): Very similar to *P. simoni* and *P. venusta*, carina variable. Vulva (Figs. 37, 38, 40, 41): Copulatory duct and spermatheca very similar to *P. simoni* and *P. venusta*; spermathecal duct with four loops; head of spermatheca bent as in *P. simoni* and

*P. venusta*; lumen of base of spermatheca large as in *P. venusta* and larger than in *P. simoni*. *Male:* (10♂). Shape, color and color pattern of body and legs as in female. Measurements: Range: Body 8.75 long, prosoma 3.5 long, 2.9 wide (Sri Lanka) to body 16.4 long, prosoma 5.6 long, 4.1 wide (INDIA: Bengal). Leg length (prosoma 3.75 long): Fe 7.08, PaTi 9.16, MeTa 11.1, total length 27.4. Male palp (Figs. 59–72): Palp and genital bulb similar to *P. simoni* and *P. venusta*; distinct ventral tibial apophysis with two-pronged tip, larger than in *P. simoni*; retrolateral tibial apophysis flat and spatula-shaped as in *P. simoni*, but with variations in length and shape, tip pointed. Great variation in distal tegular apophyses, especially in form of hook and wing.

**Remarks.**—The size range for the specimens appears to be very high. In addition, features of the male copulatory organ are surprisingly variable, but disjunct concordant features can not be found in the sample available for this study (Material from the National Collection in Calcutta was not available for study, Biswas *in litt.* 1987).

**Natural history.**—No data are available.

**Distribution.**—India, Sri Lanka, Philippines.

**Specimens examined.**—**INDIA:** *SE West Bengal*, Kanchrapara, 1♂2♀, July 1944 (AMNH); same locality, 1♂ (AMNH); *Maharashtra*, Bombay, 1♂, (OXUM 1525); same locality, 1♂, (OXUM 1522, tube 90); *Maharashtra*, Pune, 1♀ (BMNH 1899.11.2.147). **SRI LANKA:** 4♂6♀ (OXUM 1526); 1♀ (ZMHB 29225). **NEPAL:** *Dhang Dist. W Samari*, Banjang/Topal Khola (river), agricultural area, 1000–1200 m, 1♀, 23 July 83 (Martens & Schawaller leg.) (CM 211); *Mechi District*, Taplejung, Kabeli Khola (river), 900–1250 m, agricultural area, forest remains, 1♀, 1 September 83 (Martens & Daams leg.) (CM 267); *Bagmati Dist.*, Kathmandu-Valley, Balaju Park, 1♂1♀, September 69 (CM without number). **PHILIPPINES:** *Luzon*, 1♀ (ZMHB 3847). Locality unknown, “Yarkand Mission”, 1♂1♀ (OXUM).

*Perenethis symmetrica* (Lawrence 1927)

Figs. 34, 35, 58, 81

*Tetragonophthalma symmetrica* Lawrence 1927: 46; female holotype; type locality: NAMIBIA: Ongandjera; SAM B 6228; *vidi*.

*Perenethis symmetrica*, —Roewer 1955: 267.

*Pisaurellus badicus* Roewer 1961: 40, fig. 5; ♀ holotype; type locality: SENEGAL: Parc National

du Niololo-Koba; *non vidi*. Holotype not available from IFAN. NEW SYNONYMY.

*Perenethis huberti* Blandin 1975a: 382; ♀ holotype, 4♀ and 2 juv. paratypes, type locality: AFAR: Djibouti, MNHN No. 19149; *vidi*. Synonymy by Sierwald 1989a.

*Perenethis lejeunei* Blandin 1975a: 382; ♀ holotype, ♂ (= paratype); type locality: ZAIRE: Kivu; MRAC 144355; *non vidi*. Synonymy by Sierwald 1989a.

Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4361, *sub Tetragonophthalma*. Brignoli 1983: 463, *P. huberti*; page 464, *P. lejeunei*. Platnick 1993: 520.

**Taxonomic note:** The specimen figured by Blandin (1976b: fig. 8, male palp) as *Pisaurellus badicus* is not conspecific with *P. badicus* Roewer 1961, but belongs to *Perenethis simoni*. Roewer's figures (1961: fig. 5 c,e,d) of the palp establish the synonymy of *Pisaurellus badicus* with *Perenethis symmetrica*.

**Diagnosis.**—Color pattern distinctive (Blandin 1975a: figs. 8, 10): Opisthosoma dorsally with dark, lobed median band; carina of epigynum curved like eyebrows (*ch* 9); both loops of membranous copulatory duct of approximately same size (*ch* 15); embolus distinctive, broad pars pendula reaching tip of embolus (*ch* 34); smallest species of the genus.

**Description.**—Chelicerae: Inner tooth at posterior margin only slightly larger than outer tooth. Leg formula: (I-II), IV, III. Very little variation in color pattern and copulatory organs. *Female:* (11♀). Prosoma: Dorsally with dark median band, thin bright line in the middle, and laterally two broad light-yellow longitudinal bands; sternum yellow with three dark-gray spots at each side; opisthosoma dorsally with dark, lobed median band (straight in all other species of *Perenethis*); sides yellowish with irregular brown markings; venter yellowish without pattern. Legs: Femora to tibia of first three legs ventrally dark gray. Palps with black rings at joints. Measurements: Type *P. symmetrica*: Body 8.5 long, prosoma 2.5 long, 2.0 wide. Range: Body 5.7 long, prosoma 2.1 long, 1.8 wide to body 8.5 long, prosoma 2.5 long, 2.0 wide. Leg length (prosoma 2.3 long): Fe 3.1, PaTi 3.8, MeTa 4.0, total length 11.0. Epigynum (Fig. 34): Carina curved, forming "eyebrows." Vulva (Fig. 35): Copulatory duct membranous, in two large, nearly equal-sized

loops; spermatheca large, head of spermatheca round, pointing laterally; stalk thick, spermathecal duct with seven loops; base of spermatheca with small lumen. *Male:* (15♂). Shape, color and color pattern of body and legs similar to female. Legs ventrally lighter gray, only light markings at palps. Measurements: Body 5.3 long, prosoma 2.3 long, 1.7 wide to body 7.2 long, prosoma 3.0 long, 2.7 wide. Leg length (prosoma 2.3 long): Fe 4.2, PaTi 5.3, MeTa 6.2, total length 15.7. Male palp (Figs. 58, 81): Ventral tibial apophysis distinct with swollen tip; retrolateral tibial apophysis spatula-shaped, with rounded tip, little variation in the examined sample; conductor slender, edge without fringe; median apophysis with rather large, sclerotized hook; distal tegular apophysis with small hook, without wing; embolus moderately long, pars pendula nearly reaching tip of embolus.

**Natural history.**—Occurs in shrubs (Blandin 1975a).

**Distribution.**—Africa, south of the Sahara, reaching well into South Africa.

**Specimens examined.**—Types listed above. **SOUTH AFRICA:** *Transvaal*, Kruger Park, Skukuza, in thornscrub, 12♂, 15 December 1985 (AMNH); *east Transvaal*, 15 km from Klaserie, Guernsey Farm, woodland, 5♂4♀4juv♀, 19–31 December 1985 (AMNH). **TANZANIA:** *Tabora*, 1♂ (ZMHB 29226). **KENYA:** *Lake Nakuru National Preserve*, campsite in yellow fever forest, 5♂4♀, 14 May 1975 (A.J. Penniman leg.) (AMNH). **ZAIRE:** *Epulu*, 250 m, 1♂, 2 October 57 (E.S. Ross & R.E. Leech) (CASC).

### *Perenethis venusta* L. Koch 1878

Figs. 42–47, 53, 57, 75, 76

*Perenethis venusta* L. Koch 1878: 980; 3♀ syntypes; type locality: AUSTRALIA, Queensland. ♀ lectotype here designated; ZMUH, *vidi*. ♀ paralectotype: Rockhampton; ZMHB 3501 (opisthosoma missing); *vidi*. ♀ paralectotype: Peak Down; BMNH; *vidi*.

*Perenethis venusta*, –Thorell 1881: 372; ♂♀ specimens, locality: AUSTRALIA: Queensland, Cape York Peninsula; MCSN; *vidi*.

*Perenethis unifasciata*, –Thorell 1891: 61; *P. venusta* placed in synonymy of *P. unifasciata*.

*Perenethis parkinsoni* Dahl 1908: 228; ♀ holotype, type locality: PAPUA-NEW GUINEA: Bismark Archipelago, Ralum; ZMHB 29 224; *vidi*. Specimen demounted from microscope slide. NEW SYNONYMY.

*Perenethis unifasciata*, –Chrysanthus 1967: 421; several ♂♀ specimens from INDONESIA: New



Guinea, Merauke and Mindiptana; *non vidi*, figures agree with *P. venusta*.

*P. venusta*.—Chrysanthus 1967: 421, fig. 58, figure probably based on a subadult *Perenethis* female; removed *P. venusta* from synonymy of *P. unifasciata*.

*Perenethis venusta*.—Todd-Davies 1985: 104.

Catalogs: Roewer 1954, 2a: 118, as synonym of *P. unifasciata*. Bonnet 1955, 2: 4361, *sub Tetragonophthalma*, as synonym of *P. unifasciata*. Platnick 1993: 520.

**Taxonomic note.**—*P. parkinsoni* is based on a single female specimen. The female copulatory organ is very similar to Thorell's *venusta* specimen; (Figs. 45–47).

**Diagnosis.**—Color pattern and copulatory organs very similar to *P. simoni* and *P. sindica*, spermathecal duct with fewer loops than *P. simoni*.

**Description.**—Chelicerae: Inner tooth of both teeth at posterior margin distinctly larger than outer tooth. Leg formula: (II-I), IV, III. *Female*: (13♀). Coloration light yellowish-brown. Many specimens with dark-grayish coloration on the ventral side of femora, dark gray spots on the coxae and two dark-gray patches on the sternum as in *P. simoni* (Fig. 51). Dorsal color-pattern (Fig. 53) very consistent, prosoma with dark median band and light lateral zones. Two thin stripes of white hairs separate median zone from lateral zones. Opisthosoma with straight dark median band, two thin stripes of dark hair separating the median band from the light-colored lateral zones. Ventral color-pattern: Light median band caused by guanine, laterally two thin dark bands followed by two white bands formed by hair. Lateral parts of opisthosoma covered with grayish-brown hair. Measurements lectotype (ZMUH): Body 10.4 long, prosoma 3.9 long, 2.9 wide. Females slightly smaller than males, legs shorter. Range [13♀]: Body 7.7 long, prosoma 2.87 long, 2.25 wide; to body *ca.* 13 long, prosoma 4.5 long, 3.2 wide. Leg length (prosoma 4.14 long): Fe 5.96, PaTi 7.63, MeTa 8.36, total length 21.95. Epigynum in two rather distinct forms (Figs. 42, 45) both equally common. Carina branches either nearly adjoining in the middle or distinctly separated; external copulatory opening rather large. Vulva (Figs. 43, 44, 46, 47): Copulatory duct membranous, wide and saccate, forming two loops, second loop much narrower than first. Small head of spermatheca and

adjacent slender stalk of spermatheca bent dorsally; this part of the spermatheca is smaller than in *P. sindica*. Remaining spermatheca thick and heavily sclerotized; spermathecal duct either with three or four loops, loops slightly variable; size of lumen of base of spermatheca rather large but variable. Variable features of vulva not correlated with either epigynum-type. Female copulatory organ very similar to *P. sindica* and *P. simoni*. *Male*: (7♂). Coloration and color pattern as in females, somewhat lighter. Measurements [7♂]: Males slightly larger than females with longer legs; body 10.6 long, prosoma 4.0 long, 2.8 wide to body 12.0 long, prosoma 4.72 long, 3.56 wide. Leg length (prosoma 4.07 long): Fe 6.98, PaTi 9.16, MeTa 10.61, total length 26.76. Male palp (Figs. 57, 75, 76): Very similar to *P. simoni* and *P. sindica*; retrolateral tibial apophysis (Fig. 57) long and flat (spatula-shaped), tip bluntly pointed; tibial apical margin with low projection similar to *P. simoni*; median apophysis narrow, with terminal, sclerotized hook, membranous base of median apophysis enlarged; distal tegular apophysis with terminal hook and conspicuous "wing" (Fig. 76); conductor genus-typical, slender, without fringe; embolus long, whip-like with conspicuous pars pendula. Form of retrolateral tibial apophysis, median apophysis and distal tegular apophysis show very little variation within the Australian specimens; the male from Singapore very similar as well.

**Natural history.**—Occurs in grassland and forests (specimen labels; QMBA); Koh (1989).

**Distribution.**—Thailand, Singapore, Australia and Papua New Guinea.

**Specimens examined.**—AUSTRALIA: *Queensland*: Homeval, northeast Qld, 1♀ (QMBA S14 644). Eureka Ck, 1♀, 2 February 72 (QMBA S 14 634). Rundle Ra, northeast QLD, 1♀, 31 March 75 (QMBA S14 648). Doboy Ck, southeast QLD, 1♂ 1♀, 9 January 79 (QMBA S14 632). Brisbane, 1♀ with egg sac, 16 March 86 (QMBA S14 630). Bald Hills, southeast QLD, 1♀, 20 December 79 (QMBA S14 636). Bald Hills, 1♂, 10 January 80 (QMBA S14 639). Cape Hillsborough, N.P. grass area, 1♀, 5 January 75 (QMBA S14 643). Bundaberg forest, southeast QLD, 1♀ (QMBA S14 629). Newroy Is. N.P., 1♂, 14 February 75 (QMBA S14 638). Currumbin, southeast QLD, 1♂, 11 January 80 (QMBA S14 633). Weipa, 1♂, 7 February 75 (QMBA S14 641). 12 samples with juveniles from



Queensland Museum. **SINGAPORE:** Mac Ritchie Reservoir, in grass, 1 ♀ (Koh 89.07.13.08). Malcolm Road, grassy waste land, 1 ♂, (Koh 85.08.24.01). **PAPUA NEW GUINEA:** Madang Province, Sapi Forest Reserve, 30 km west of Madang, 5°12'S, 145°30'E, 1 ♀, 4 July 1988 (W.J. Pulawski) (CASC). Vogelkop, Manokwan, 75 m, 1 ♀, 21 July 1951 (D. Elmo Hardy) (BPBM). Waris, 450 m, 1 ♀, VII-VIII (T.C. Maa) (BPBM). **THAILAND:** 8 mi SE Saraburi, 100 m, 1 ♂, 28 July 62 (E.S. Ross & D.Q. Cavagnaro) (CASC).

**Special forms.**—The material examined for this study contained two males that cannot be placed in any described *Perenethis* species. Due to the uncertainty of species discrimination between *P. fascigera*, *P. simoni*, *P. sindica* and *P. venusta* on one hand, and the unusual variability in *P. sindica* on the other hand, descriptions of new species-group taxa do not appear justified at this point.

Form I (Figs. 77, 78): Male from Turkey: Smyrna, OXUM. The specimen is similar to *P. simoni*, but the retrolateral tibial apophysis possesses an anterior basal projection. Form II (Figs. 79, 80): Male from Nepal [Dhading Dist, between Kagune and Samari Banjyang, 800–1000 m, 23 July 83, agricultural area, CM]. In this specimen the shape of the retrolateral apophysis is different and does not fit the overall pattern found in *P. sindica*. Since the shape of the retrolateral tibial apophysis is often species-typical in Pisauridae, this specimen could belong to a species distinct from *P. sindica*; it may represent the male of *P. dentifasciata*.

#### NOMINA DUBIA

##### *Perenethis brevipes* (Strand 1906)

*Tetragonophthalma brevipes* Strand 1906: 685; holotype juvenile (lost), type locality: Sudan, Harerge Mountains; Naturkunde-Museum Stuttgart. *Perenethis brevipes*, —Roewer 1955: 267. *P. brevipes*, —Blandin 1975a: 384; *nomen dubium*

##### *Ctenus marginatus* Walckenaer 1847

*Ctenus marginatus* Walckenaer 1847: 402, ♀ ?holotype; type locality: Solomon Islands; type presumed lost. *Thalassius marginatus*, —Simon 1891: 299.

Walckenaer compares the specimen to *Pisaura mirabilis*. This could suggest that Walckenaer's specimen was congeneric with *Perenethis* (general color pattern and habitus). Simon's (1891) placement of this species in

the genus *Thalassius* was rejected (Sierwald 1987).

##### *Perenethis rectifasciata* (O. Pickard-Cambridge 1885)

*Ocyale rectifasciata* O. Pickard-Cambridge 1885: 78; juvenile male holotype; type locality: north-east PAKISTAN or north-west INDIA ("Murree to Sind valley and Sind valley"); OXUM; *vidi*. *Pisaura rectifasciata*, —Simon 1898a: 289. Catalogs: Roewer 1954, 2a: 121, *sub Pisaura*. Bonnet 1955, 2: 3681, *sub Pisaura*.

Based on eye-pattern and number of teeth at the chelicerae, the subadult male is a member of the genus *Perenethis*. Color-pattern faded, most spines lost. *P. rectifasciata* is here considered a *nomen dubium*.

##### *Perenethis unifasciata* (Doleschall 1859)

*Dolomedes unifasciata* Doleschall 1859: 10; ♀ holotype lost; type locality: Indonesia: Amboina. *Perenethis unifasciata*, —Thorell 1891: 61. *Tetragonophthalma unifasciata*, —Strand 1911: 165, ♀ from INDONESIA: Kepulauan Aru Islands, Pulau Kobroor. Specimen not in SMFD (*fide* Chrysanthus 1967). Catalogs: Roewer 1954, 2a: 118. Bonnet 1955, 2: 4361, *sub Tetragonophthalma*.

According to the collection catalog in the Museum for Natuurlijke Historie in Leiden the female specimen figured in Doleschall's publication (1859, fig. 6) never arrived in Leiden (van der Hammen pers. comm. 1982). Therefore, no actual type-specimen exists. The specimen figured could be conspecific with *venusta*. *P. unifasciata* is here considered a *nomen dubium*.

##### *Maypacius* Simon 1898 Figs. 82–87, 91–96

*Maypacius* Simon 1898a: 292. Type species, by original designation, *Maypacius vittiger* Simon 1898b: 13; female holotype, Madagascar & Africa.

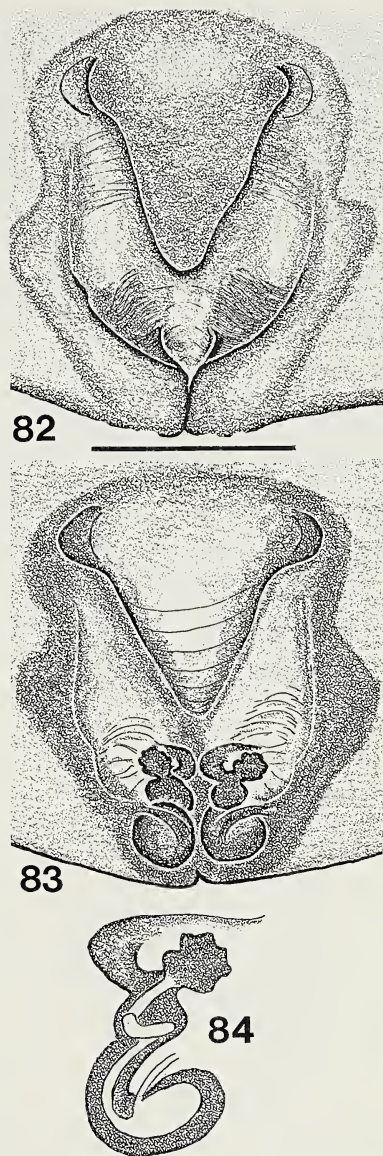
Blandin (1975a, 1978b) recognized nine species in the genus *Maypacius* and listed a total of 21 specimens, only six of them males; five species are known from females only, two from males; for two species both sexes are recognized. Species: *Tetragonophthalma bilineatus* Pavesi 1895, ♀ known; *Maypacius christophe* Blandin 1975 (1975a), ♀ known; *Maypacius curiosus* Blandin 1975 (1975a), ♂ known; *Maypacius gilloni* Blandin 1978 (1978b), ♂ ♀ known; *Maypacius kaestneri*



Roewer 1955, ♂ ♀ known; *Maypaci* *petrunkevitchi* Lessert 1933, ♀ known; *Maypaci* *roeweri* Blandin 1975 (1975a), ♂ known; *Maypaci* *stuhlmanni* Bösenberg & Lenz 1894, ♀ known; *Maypaci* *vittiger* Simon 1898 [Simon 1898b: 13], ♀ known. *Maypaci* *vittiger* was synonymized with *Tetragnophthalma bilineatus* Pavesi 1895 by Simon (1906: 1169); Roewer (1955: 153) listed *M. vittiger* as junior synonym of *Maypaci* *bilineatus*; Blandin (1974a: 309; 1975a: 385) removed *M. vittiger* from the synonymy of *M. bilineatus*.

**Diagnosis.**—Two equally-sized cheliceral teeth (*ch* 0, 1), short copulatory duct (*ch* 15), short spines (*ch* 6), and the following autapomorphic characters: Strongly procurved AER (*ch* 2), ALE on tubercles and located nearly beneath AME; conductor short (*ch* 23), with specialized apical region with two guiding lamellae (*ch* 28). Synapomorphic characters: Two cheliceral teeth at retromargin (*ch* 0) and retrolateral peak at tegulum (*ch* 21) shared with *Polyboea* and *Perenethis*; conductor with two guiding lamella (*ch* 28), pit in dorsal branch of distal tegular apophysis (*ch* 29) and shape of sclerite A shared with *Polyboea* (*ch* 31).

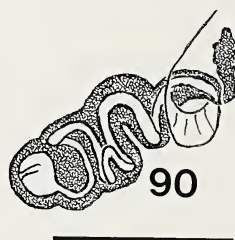
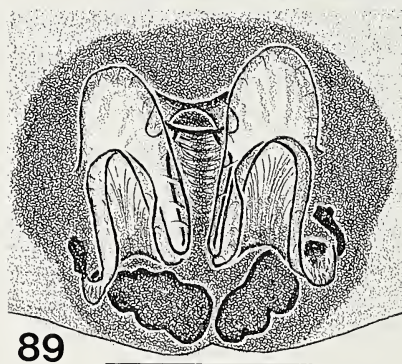
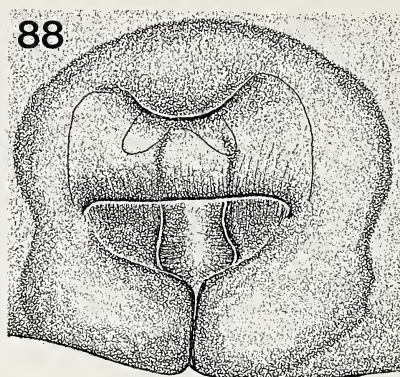
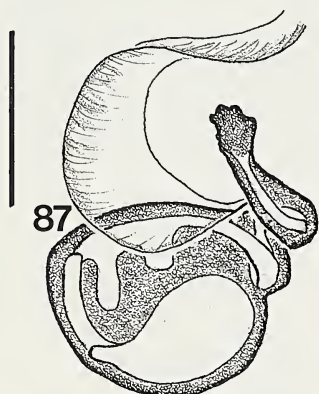
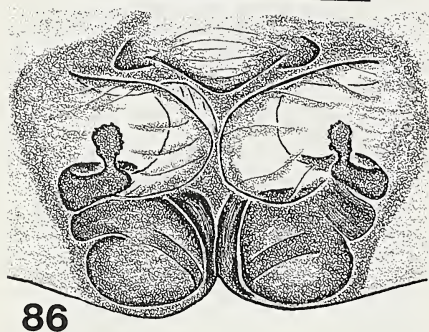
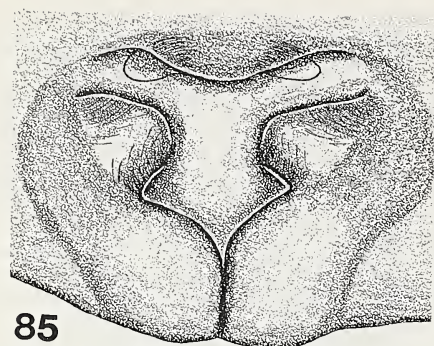
**Description.**—Based on *M. kaestneri*, *M. petrunkevitchi*, and *M. roeweri*. Measurements: *M. kaestneri*: ♀: Body 12.43 long, prosoma 3.56 long, 2.6 wide (MRAC 142.407). Leg length: Fe 6.6, PaTi 7.8, MeTa 8.7, total length 23.2. *M. petrunkevitchi*: ♀: Body 13.45 long, prosoma 2.9 long, 2.18 wide. Leg length: Fe 5.45, PaTi 6.6, MeTa 7.2, total length 19.25 (MRAC 145.395). *M. roeweri*: ♂: Body 11.81 long, prosoma 3.45 long, 2.7 wide. All legs broken off. Eye pattern: AE in two rows (AER extremely procurved); ALE on tubercles, in front of AME and only slightly further apart from each other than AME; PLE=AME>PME=ALE. Eyes small compared to body size, PME:AME = 0.7–0.8; AME:ALE = 1.5. Chelicerae: Posterior margin with two equally-sized teeth, teeth closer to outer edge of chelicerae and wider spaced than in *Perenethis*. Spine pattern identical with *Charminus camerunensis*. Spine length: Spines very short; spine length:tibia width = 1. Epigynum (*M. petrunkevitchi* and *M. kaestneri*, Figs. 82, 85): Continuous carina weakly developed, anterior edge conspicuous, carina straight or recurved (strongly recurved in



Figures 82–84.—*Maypaci petrunkevitchi* from Rwanda (MRAC 145.395). 82, Epigynum; 83, Vulva; 84, Left spermatheca, dorsal view. Scale lines: 82, 83 = 0.5 mm; 84 = 0.2 mm.

*M. petrunkevitchi*); fossae mesal to copulatory opening. Vulva (Figs. 83, 84, 86, 87): Membranous copulatory duct short, forming single curve; *M. petrunkevitchi*: Copulatory duct sclerotized close to the spermathecae, head of spermatheca pointing anteriorly, spermathecal duct forming single loop, base of spermatheca with small lumen; *M. kaestneri*: Head of spermatheca bent, spermathecal duct with two loops, base of spermatheca with large lumen.





Figures 85–87.—*Maypacijs kaestneri* from Ghana (MRAC 142.407). 85, Epigynum; 86, Vulva; 87, Left spermatheca, dorsal view. Scale lines: 85, 86 = 0.5 mm; 87 = 0.2 mm.

Figures 88–90.—*Polyboea vulpina* from Singapore (NMSC). 88, Epigynum; 89, Vulva; 90, Left spermatheca, dorsal view. Scale lines: 88, 89 = 0.5 mm; 90 = 0.2 mm.

Male palp (based on *M. roeweri*, Figs. 91–96): Retrolateral tibial apophysis pointed, directed forward (perpendicular in *M. curiosus*); tegulum with conspicuous, retrolateral peak; short conductor with narrow base and uniquely enlarged tip, embolus resting between two lamellae; distal tegular apophysis with hook and wing, dorsal branch of distal tegular apophysis with pit as in *Polyboea*; sclerite A large, forked, similar to *Polyboea*; distal sclerotized tube similar to *Polyboea*; embolus

short, with wide pars pendula, about  $\frac{1}{2}$  embolus length. For the cladistic analysis, characters for the male of *M. kaestneri* were taken from Blandin's figure (1975a: 389, fig. 21, 22).

**Natural history/habitat.**—Occurs in the savanna, found in vegetation (Blandin 1978b).

**Specimens examined.**—*M. roeweri*: **ZAIRE**: Kivu, Uvira, Mugesera, 1♂ paratype (MRAC 145.058). *M. petrunkevitchi*: **RWANDA**: Burgesera, Biharagu, found in dense field vegetation, 1♀ (MRAC 145.395); Butare, 2♀ (MRAC 140.720). *M. kaestneri*: **GHANA**: Legon, 1♀ (MRAC



142.407). **CONGO:** *Faradje*, 1♀ (MRAC 145.400).

*Polyboea* Thorell 1895

Figs. 88, 90, 97–101

*Polyboea* Thorell 1895: 228. Type species, by original designation, *Polyboea vulpina* Thorell 1895: 229, juvenile male holotype, Burma: Rangoon).

The genus is based on a subadult male of the type species from Burma. Male and female copulatory organs from specimens collected in Singapore are figured here for the first time. Currently, the genus is monotypic. The Asian pisaurid genus *Eurychoera* Thorell 1897 (listed in the Pisaurinae by Roewer, 1955: 115) from Singapore (Koh 1989: 97) is not closely related to *Polyboea*.

**Diagnosis.**—AER procurved (*ch* 2), two equally-sized cheliceral teeth (*ch* 0) and the following autapomorphic characters: ALE significantly larger than PME (*ch* 3) and AME (*ch* 4); chelicerae longer than in all other perenethine genera; absence of the two paired short spines apically at the ventral side of the tibia. Since the genus is currently monotypic, characters listed here may be apomorphic at species level. Synapomorphic characters: Two cheliceral teeth at retromargin (*ch* 0) and tegulum with retrolateral peak (*ch* 21) shared with *Perenethis* and *Maypaci*; copulatory duct with two wide membranous loops shared with *Perenethis* and *Charminus camerunensis* (*ch* 14), conductor with two guiding lamellae (*ch* 28), pit in dorsal branch of distal tegular apophysis (*ch* 29) and shape of sclerite A shared with *Maypaci* (*ch* 31).

*Polyboea vulpina* Thorell 1895

Figs. 88–90, 97–101

*Polyboea vulpina* Thorell 1895: 229.

*Polyboea vulpina*, –Workman & Workman 1897: 97 (= *Ocyale hirsuta* on plate 97.); *non vidi*.

*Polybaea[sic] vulpina*, –Simon 1898a: 289, 296

*Polyboea vulpina*, –Hasselt 1899: 174

*Polyboea vulpina*, –Koh 1989: 100 (color photo of ♂)

Catalogs: Petrunkevitch 1928: 102, as *Polybaea*.

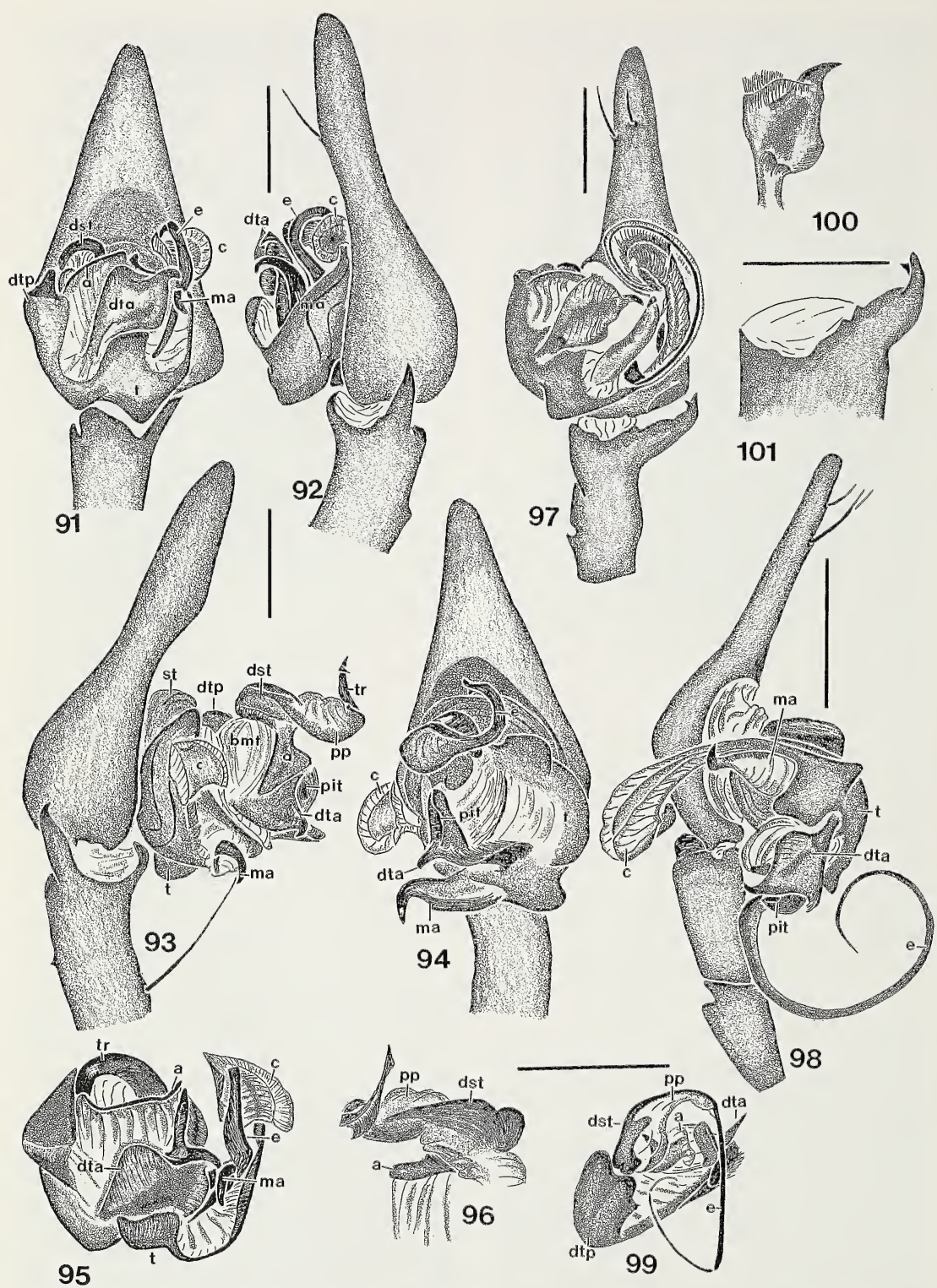
Roewer 1954, 2a: 122, as *Polybaea*. Bonnet 1955, 2: 3751. Genus listed: Brignoli 1983: 461, *Polybaea*; Platnick 1989: 393, *Polybaea*; Platnick 1993: 521, *Polyboea*.

**Diagnosis.**—Chelicerae large, spines long, tibia lacks apical ventral spine pair; epigynal folds parallel and apart from each other anteriorly; carina forming lip with straight pos-

terior edge; long conductor with curved tip, similar to conductor in the west African *Maypaci* *gilloni* (Blandin 1978b: fig. 2).

**Description.**—Eye pattern: AER procurved; AER nearly as wide as PER, ALE>PLE=PME>AME. AME conspicuously smaller than PME, PME:AME = 1.6; AME:ALE = 0.5. Chelicerae: Posterior margin with two nearly equally-sized teeth, teeth closer to outer edge of chelicerae and wider spaced than in *Perenethis*; chelicerae in both sexes longer than in other Pisauridae, prosoma width:chelicerae-length = 1.7; compare to *Maypaci* *roeweri* ♂: prosoma width:chelicera length = 2.7; *petrunkevitchi* ♀: 2.39; *kaestneri* ♀: 3.3. Spine pattern (Table 6): Pro- and retrolateral femoral spines variable within a single specimen. The absence of two paired short spines apically at the ventral side of the tibia is unique within the Pisaurinae. Spine length: Spines very long; spine length:tibia width = 6.5. *Female*: (1♀). Light orange-yellow, pattern faded (but see male coloration below). Measurements: Body 6.03 long, prosoma 2.5 long, 2 wide. Epigynum (Fig. 88): Epigynal folds parallel and apart from each other anteriorly; adjoining posteriorly; carina forming lip with straight posterior edge, overhanging copulatory opening; fossae close together, mesal to the copulatory openings. Vulva (Figs. 89, 90): Copulatory duct wide and membranous, forming two saccate loops as in *Perenethis*, first loop larger than second loop; head of spermatheca bent, pointing anteriorly; spermathecal duct with four loops; base of spermatheca with small lumen. *Male*: (7♂). Carapace, legs and sternum light orange-yellow, abdomen dorsally with distinct gray-beige Y-shaped figure, the anterior lateral stripes of the Y meet behind the heart, a pair of distinct white spots lateral to the median tail-stripe of the Y. Abdomen ventrally with two parallel narrow dark lines. Measurements: Body length 9.16–10.6, prosoma 3.08–3.6 long, 2.36–2.96 wide. Leg length (prosoma 3.6 long): Fe 6.3, PaTi 8.16, MeTa 9.4, total length 23.8. Male palp (Figs. 97–101): Retrolateral tibial apophysis perpendicular, tip with two pointed ends; tegulum with conspicuous peak at retrolateral corner; long conductor with narrow base and broad tip; tip curved in a spiral; two long guiding lamellae, especially visible in the expanded palp; distal tegular apophysis small, with fringed wing; sclerite A





Figures 91–101.—*Maypacijs roeweri* and *Polyboea vulpina*. 91–96, *Maypacijs roeweri* from Zaire (MRAC 145.058). 91, Unexpanded left palp, ventral view; 92, Unexpanded left palp, retrolateral view; 93, Expanded right palp, retrolateral view, pit indicates pit in distal tegular apophysis; 94, Expanded right



large with the straight edge visible in the unexpanded palp as in *Maypaci*, forked distal end towards the distal sclerotized tube; embolus moderately long; pars pendula short and wide as in *Maypaci*.

**Natural history/habitat.**—Hasselt (1899) and Koh (1989) report that *P. vulpina* occurs in grasses and low shrubs, building “large, three-dimensional webs that may be connected with one another.” This may indicate some form of colonial habit.

**Distribution.**—Known from Thailand, Malaysia and Singapore.

**Specimens examined.**—**SINGAPORE:** no locality given, 1♀ (NMSC 1990.600). Mac Ritchie Reservoir, grasses, 1♂ (Koh 77.01.01.03). **THAILAND:** *Khao*. Yai Nat. Park, 750 m, 2♂, 26 July 1962 (E.S. Ross & D.Q. Cavagnaro) (CASC). 10 mi N Saraburi, 100 m, 1 juv.♂, 11 July 1962 (E.S. Ross & D.Q. Cavagnaro) (CASC). 20 mi S.E. Chantaburi, 75 m, 2♂, 1 August 1962 (E.S. Ross & D.Q. Cavagnaro) (CASC). **MALAYSIA:** Fraser’s Hill, 4200 m, 1♂, 2juv., 17 June 62 (E.S. Ross & D.Q. Cavagnaro) (CASC).

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palp, ventral view; 95, Unexpanded left palp, embolic division, top view; 96, Expanded right palp, embolic division, lateral view. 97–101, Left male palp of *Polyboea vulpina* from Singapore (Coll. Koh), Singapore. 97, Unexpanded, ventral view; 98, Expanded, prolateral view, pit indicates pit in distal tegular apophysis; 99, Same, embolic division, top view; 100, Apophysis distal tegular apophysis; 101, Retrolateral tibial. Scale lines = 0.5 mm.

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## RESEARCH NOTE

### A NEW GENERIC SYNONYMY IN SCORPIONS: *SCORPIOBUTHUS* WERNER = *UROPLECTES* PETERS (SCORPIONES, BUTHIDAE)

The genus *Scorpiobuthus* was briefly described by F. Werner (1939) from specimens lacking locality data, and it has been more or less forgotten since that time. The genus was monotypic, containing only the species *Scorpiobuthus apatris* Werner 1939, described in the same paper. Interestingly, Werner (1939) did not assign *Scorpiobuthus* to a family, but indicated it was close to *Buthoscorpio* Werner 1936 (which he regarded as a member of the Scorpionidae). The type specimens have not been subsequently studied, and no new specimens have been reported in the last 57 years. The genus name was rediscovered by Francke (1985) and listed among valid scorpion generic names in his conspectus, under Buthidae. However, it was not included in recent generic keys to buthids or other families (Stahnke 1972; Sissom 1990).

Through the kindness and enthusiastic support of Dr. Franz Krapp, the curator of the Lower Invertebrates Division of the Zoologisches Forschungsinstitut und Museum Koenig (Bonn, Germany), we were able to examine the type specimens of *S. apatris* which are deposited in this Museum. The type series consists of two adult female syntypes (dried and later rehydrated; partially damaged), Nos. 82 and 83. We hereby designate No. 83 as lectotype and No. 82 as paralectotype.

First of all, *Scorpiobuthus* is indeed a buthid. The sternum of *Scorpiobuthus* was reported to be subpentagonal (Werner 1939), but examination of the types reveals that the lateral edges of the structure are moderately convergent anteriorly—in fact, the sternum could be regarded as subtriangular, although not extremely so. Further, as in other buthids, the anterior aspect of the sternum bears a small lobe-like structure that is separated from the main portion by a distinct groove. Upon study of additional characters, it became clear to us

that the specimens are referable to *Uroplectes* Peters 1862. They share the following diagnostic characters with members of that genus: (1) the alpha-pattern of dorsal trichobothria of the pedipalp femur; (2) the presence of a distinct subaculear tooth; (3) the absence of denticles on the undersurface of the cheliceral fixed finger; (4) enlarged proximal pectinal teeth in the female (found in many *Uroplectes*); (5) the dentition pattern of the pedipalp chela fingers; (6) reduction of the carapacial carinae; and (7) the presence of tibial spurs on legs III and IV. If the sternum is regarded as subtriangular, the specimens trace easily to *Uroplectes* in Sissom's (1990) key to buthid genera. We therefore propose the following synonymy: *Scorpiobuthus* Werner 1939 = *Uroplectes* Peters 1862.

The genus *Uroplectes* is widespread in southern and eastern Africa. Checking keys published for South Africa (Hewitt 1918; Lawrence 1955), East Africa (Probst 1973) and Namibia (Lamoral 1979), we discovered a close match with *Uroplectes chubbi* Hirst 1911. This species is unusual in that all five metasomal segments are smooth and coarsely punctate, a feature found in the two specimens of *Scorpiobuthus apatris*. The specimens match other details provided in a brief description of *U. chubbi* by Hewitt (1918). Consequently, we propose the following species synonymy: *Scorpiobuthus apatris* Werner 1939 = *Uroplectes chubbi* Hirst 1911.

On a final note, the status of *U. chubbi* is somewhat uncertain and needs clarification. Hewitt (1918) suspected that *U. chubbi* was a junior synonym of *U. jutrenkai* Penther 1900. However, at the bottom of the same page he suggested that *U. chubbi* had affinities with *U. xanthogrammus* Pocock 1897, which was suggested to be a "variety" of *U. fischeri* (Karsch 1879) by Kraepelin (1913). Hewitt then stated



that *U. chubbi* was probably a variety of *U. fischeri* as well, perhaps unaware that Birula (1915) had accepted *U. xanthogrammus* as a valid species. More recently, *U. xanthogrammus* was regarded as a subspecies of *U. fischeri* by Probst (1973), and *U. jutrenkai* was synonymized with *U. vittatus* (Thorell 1876) by Newlands (1970). The latter author appeared to consider *U. chubbi* distinct from *U. vittatus*. Finally, Lamoral & Reynders (1975) recognized all three taxa (*U. vittatus*, *U. chubbi*, and *U. fischeri*) as distinct species. Clearly, the situation requires further study.

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## RESEARCH NOTE

### SYNONYMY OF THE PSEUDOSCORPION *CHERNES INSUETUS* WITH *AMERICHERNES OBLONGUS* (CHELONETHI, CHERNETIDAE): AN UNESTABLISHED INTRODUCTION TO BRITAIN

*Chernes insuetus* was described by O.P. Cambridge (1892) from two specimens found in an oil mill in Dover, Kent (England). The mill was later demolished (Kew 1911) and this species has not been recorded since. Kew, who examined one of the types, noted that this species belonged to “a group with polished integuments, almost simple bristles, non-granulate tergites, and with a tactile hair near extremity of tibia IV.” Although this would have placed *C. insuetus* in the Lamprochernetinae (as then defined), Beier (1932) listed it as a doubtful species of *Allocheres* Beier 1932, in which he was followed by Roewer (1937).

The name *insuetus* did not appear again in the literature until Legg & Jones (1988) synonymized it with *Lamprochernes chyzeri* (Tömösváry 1882). Although no justification was given for this synonymy, it was accepted as the *status quo* by Harvey (1991). However, the identification of *insuetus* with *chyzeri* is hard to accept in view of the fact that Kew – a competent specialist – had examined British material of both species and found them to be quite distinct.

In 1980 I was able to study the two female syntypes of *Chernes insuetus*, deposited in the Hope Entomological Collections of Oxford University Museum (HECO). The specimens were lent to a third party at the Natural History Museum, London, under whose supervision they were studied. Afterwards, the types were left on a desk, to be mailed the next day. Unfortunately, they disappeared before this could be done and must be presumed lost. The material of *C. insuetus* which Cambridge sent to E. Simon (who first identified it as new to science) was evidently returned, there being

no trace of this species in the collections of the Muséum national d'Histoire naturelle, Paris.

Although the spermathecae could not be examined, the external morphology of the types of *C. insuetus* was found to agree with Muchmore's (1976) redescription of *Americhernes oblongus* (Say 1821). *Chernes insuetus* Cambridge is therefore considered to be a junior subjective synonym of *A. oblongus*.

#### *Americhernes oblongus* (Say 1821)

*Chelifer oblongus* Say 1821:64. Neotype ♂ from Havana, Illinois, USA; designated by Hoff (1949) (Illinois Natural History Survey, not examined).

*Americhernes oblongus* (Say): Muchmore 1976: 153–156, figs. 3–9; Harvey 1991:542 (complete synonymy up to 1989).

*Chelifer communis* var. *pennsylvanicus* Ellingsen 1910:366 (synonymized by Muchmore 1991:80).

*Chelifer* n. sp. Cambridge 1884:103.

*Chernes insuetus* Cambridge 1892:225–226, pl. C fig. 17; Kew 1916:130–131. Syntypes 2♀, from debris and refuse in oil mill, Dover, Kent, England, leg. W.P. Haydon, 1880 (HECO, examined; now lost). NEW SYNONYMY.

*Chelifer (Chernes) insuetus* (Cambridge): Kew 1911:41 (footnote 1).

*Allocheres(?) insuetus* (Cambridge): Beier 1932: 154; Roewer 1940:298.

*Lamprochernes chyzeri* (not Tömösváry): Legg & Jones 1988:102 (in part); Harvey 1991:588 (in part).

As the derivation of its junior synonym implies (Latin *insuetus*, unaccustomed), Cambridge (1884) regarded this species as alien to the British fauna, perhaps having been imported with oilseeds used in the mill. *Americhernes oblongus* is widely distributed in the United States (Muchmore 1976; Harvey



1991), and it is likely that the Kentish population originated from the eastern seaboard of North America. It is worth noting that they were found in company with the first known British specimens of *Withius piger* (Simon 1878) (syn. *Chelifer subruber* Simon 1879), another introduced species (Cambridge 1884, 1892).

*Americhernes* Muchmore 1976 is currently known from the Americas, Australia and the Pacific (Muchmore 1976; Harvey 1990), but there have been no subsequent records of this genus from Europe. Although several European pseudoscorpions have been found in North America (Muchmore 1972), this appears to be the first record of an introduction in the opposite direction. In this case, however, it is clear that *A. oblongus* did not become established in Britain.

#### ACKNOWLEDGMENTS

I am grateful to A. Smith for arranging the loan of the syntypes of *Chernes insuetus* and to I. Lansbury for his help during a recent visit to Oxford University Museum. Mark Harvey and Bill Muchmore are thanked for very helpful reviews of the manuscript.

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 33, 34, *A-us y-us*, male. Scale = 1.0 mm.

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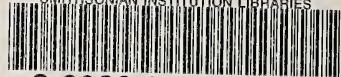


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